



PHD

**Conservation biology of the endangered St. Helena  
Plover *Charadrius sanctaehelenae***

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**Conservation biology of the endangered St. Helena  
Plover *Charadrius sanctaehelenae***

Volume 1 of 1

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A thesis submitted for the degree of Doctor of Philosophy

University of Bath  
Department of Biology and Biochemistry  
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## Abstract

Oceanic islands contribute significantly to global biodiversity due to the high levels of endemism they exhibit. Many island species have, however, become extinct following the arrival of humans, and many others remain threatened. This thesis focuses on one of these threatened island species; the St. Helena Plover, *Charadrius sanctaehelenae*.

The objectives of my PhD were threefold: to understand the current status of the St. Helena Plover, to investigate aspects of its environment that may threaten its persistence, and to compare conservation options. Observational data were used to understand how variation in the environment influences the plover's distribution and demography. This information was used to inform a controlled trial investigating the use of nest exclosures as a way to improve productivity. New understanding of the species' population ecology was brought together to create a stochastic meta-population model. This model was used to understand the influence of demographic and life history parameters on the population growth rate and to compare alternative conservation options.

Indicators of the future status of the St. Helena Plover population appear mixed; with numbers predicted to decline slowly, but with a high chance of species persistence over the timeframe simulated, 50 years. Nest predation by introduced species, predominately cats, was predicted to suppress nest survival and bring productivity at some sites below that required for population stability. The use of nest exclosures did not increase nest survival and led to a decrease in adult survival. Habitat characteristics were more important in determining the species distribution than influencing its demography. The plovers appeared to select breeding habitat to maximise the visibility from the nest and the accessibility of invertebrate prey. Simulations suggested that predator control would have a large beneficial effect on the population growth rate and that concurrent habitat improvement would have greater than additive benefits. Targets for conservation management include Deadwood Plain; predator control as this key site was predicted to lead to the largest increase in the overall population growth rate, and Man and Horse; there may be potential at this site to increase adult survival, which was found to be the most influential demographic parameter.

## Introduction

### Islands

Islands are important. They are important for science, they are important for biodiversity and their biodiversity is threatened. Islands with their simplified ecosystems and often long isolation have proven instrumental in the development of the key theories that underpin much of modern ecology, notably evolutionary theory and biogeography.

“It is not too much to say that when we have mastered the difficulties present by the peculiarities of island life we shall find it comparatively easy to deal with the more complex and less clearly defined problems of continental distributions”  
(Island Life, Wallace 1902, quoted in Whittaker and Fernández-Palacios 2007)

The long isolation of islands resulted in a wealth of convergent evolutionary pathways, where species of vastly different lineages come to inhabit similar ecological niches; and so serve as essentially multiple replicates of the evolutionary process. Because of this, islands are full of unique and unusual species and it is this aspect that most captures the human imagination. Nevertheless, the flora and fauna of islands share a great many characteristics. These include; high initial dispersal ability and its subsequent loss, size change, and behavioural change; for instance reduction in clutch size in birds (Whittaker and Fernández-Palacios 2007; Williamson 1981).

Islands are the best place to observe adaptive radiation, for instance at least 100 Hawaiian lobeliads are thought to descend from a single colonisation event (Gillespie and Clague 2009). High levels of adaptive radiation, as well as peripatric speciation, have resulted in high levels of endemism on islands. Endemic bird areas are defined as areas supporting two or more restricted range bird species ( $\leq 50,000 \text{ km}^2$ ), and 103 out of 218 of these areas are on islands (Long et al. 1996). Islands also harbour relic lineages that have subsequently died out elsewhere. *Amborella trichopoda* is an ancient plant species found on New Caledonia. It is the only member of a sister group to all other flowering plants, the split between these groups occurred at least 130 million years

ago. Despite high levels of endemism, overall species richness on islands is generally lower compared to similar sized areas of mainland and species composition is disharmonic, i.e. some groups are missing and some over sampled (Gillespie and Clague 2009).

MacArthur and Wilson (1967) hypothesised that species richness on islands was a balance between immigration from mainland populations and extinction, and that these relationships were dependent primarily upon isolation from continental landmasses and island size respectively. Their original theory provoked much theoretical and empirical work and has been refined and alternatives proposed since this time, including the rescue effect (Brown and Kodric-Brown 1977) and the species-energy theory (Wright 1983). Due to habitat destruction and fragmentation many mainland species now exist in small patches of suitable habitat surrounded by large areas of unsuitable habitat, and soon after its publication ecologists began comparing these isolated habitat patches to the islands of MacArthur and Wilson's theory. This comparison was used to address questions about the design of nature reserves: how many reserves are required to protect a species, how big should they be, and how should they be connected? The theory appeared to give practical answers to difficult questions, and therefore resonated with conservation practitioners and policy makers. Although the application of island theories to reserve design is no longer so strongly supported (Whittaker and Fernández-Palacios 2007), it remains an important illustration of the translation of scientific theory into conservation practice.

### **Threats to Islands**

Sadly, islands are also characterised by high levels of historic extinctions, and currently threatened species (Johnson and Stattersfield 1990; Lee and Jetz 2011). Eighty percent of bird extinctions since 1600 were from islands (Johnson and Stattersfield 1990), and although less than one fifth of bird species are restricted to islands, island forms account for over half of all threatened bird species (Birdlife International 2011a). By calculating the proportion of species missing from the avian fossil record Pimm (1994) estimated that 90-110 birds species are now extinct out of 125-145 species present prior to human colonisation in Hawaii.



Historic island extinctions and current declines are largely due to anthropogenic change and can be explained by the same issues that dominate conservation globally: habitat change and fragmentation, unsustainable resource use by humans and introduced species (Brook et al. 2003; Diamond et al. 1989; Johnson and Stattersfield 1990). Although introductions are not more frequent on islands than on the continental mainland, their impacts on indigenous island species are often more severe (Clavero and García-Berthou 2005; Hilton and Cuthbert 2010), largely due to the absence of a shared evolutionary history; as some groups of species, such as vertebrate browsers and predatory mammals, are often missing from islands (Gillespie and Clague 2009). Island species may also be at elevated risk of extinction due to small population size (Reaser et al. 2007) and range size (Lee and Jetz 2011). Introduced species are thought to be the largest contributor to past island bird extinctions. The probability that a bird species has been lost correlates with the number of different predators species introduced since European colonisation (Blackburn et al. 2004), and species introductions are currently occurring at an unprecedented rate (Mack et al. 2000). The rate of species introductions is such that bird species richness on oceanic islands has remained constant despite widespread extinction of endemic forms, and for vascular plants introductions far outweigh extinctions (Sax et al. 2002). This process has led to the loss of biodiversity on islands and conforms to a general trend towards homogenisation of ecosystems around the world due to anthropogenic actions (Benton et al. 2003; McKinney and Lockwood 1999; Pimm et al. 1994).

The impacts of invasive species on island life forms can be dramatic, costly and often unexpected. *Rattus* species are now widespread amongst the world's islands, with 82 % of the 123 major island groups invaded (Atkinson 1985). Black rats *Rattus rattus* are thought to be responsible for the extinction of three vertebrate species within two years of arrival on Big South Cape Island, New Zealand (Bell 1978, cited in Courchamp and Chapuis 2003). The golden apple snail *Pomacea comdicolata* was deliberately introduced to the Philippines in the 1980's. This species feeds on rice and the cumulative cost to rice farmers to 1990 was US \$425-1200 Ma (Naylor 1996). This snail species also supports parasitic worms, leading to fatalities in humans (Lo Re 2003, cited in Reaser et al. 2007). The Macquarie Island parakeet *Cyanoramphus novaezelandiae* persisted for 60 years following the introduction of cats *Felis catus* to the island. However, within 10 years of the subsequent introduction of rabbits

*Oryctolagus cuniculus* the parakeet was extinct. It is hypothesized that the rabbits provided the cats with abundant food throughout the year and allowed their population, and thus their impact on the parakeet population, to vastly increase (Taylor 1979).

## **UK Overseas Territories**

Unknown to many residents of the UK mainland, the UK retains governance of 14 Overseas Territories (UKOTs). These territories are scattered across the globe from South Georgia and the South Sandwich Islands in the Antarctic, to the British Indian Ocean territories (Figure 1). All of the territories except Gibraltar are islands, and therefore share the island characteristics and threats described above.

The UKOTs together have more endemic species and more threatened species than mainland Europe. They support 34 species of globally threatened birds species, and 22 of the 24 endemic bird species are threatened (Hilton and Cuthbert 2010). UKOTs are of particular importance for breeding seabirds and sea turtles; for example, 90 % of global population of black-browed albatross *Diomedea melanophris* breed on the Falklands and South Georgia, and Ascension Island holds the second largest breeding colony of green turtles in the Atlantic (Oldfield 1999). The UKOTs have also suffered from recent extinctions, with ten endemic bird species becoming extinct in historic times (BirdLife 2009). The threat posed by introduced species to UKOTs was highlighted recently by the review of Hilton and Cuthbert (2010). This paper shows the pivotal role cats and rodents have played, and continue to play, in the extinctions of endemic bird species and the major depletion of sea bird colonies from the overseas territories.

The UK signs international conventions, such as the Convention of Biological Diversity, on behalf of its Overseas Territories. The ability of the UKOTs to protect their natural assets varies, however, both in terms of finance and expertise; leaving the UK with a responsibility to support nature conservation within the territories. Although the UKOTs have been somewhat neglected given their global importance, the UK is working towards establishing effective conservation measures in the Overseas Territories, for example through the Overseas Territories Environment Programme. Recent conservation initiatives include the designation of the world's largest marine

protected area in 2010 in the British Indian Ocean Territory (Anon 2010a), and the removal of cats from Ascension Island in 2004 (Hughes et al. 2008).



**Figure 1** – *UK Overseas Territories.*

### **St Helena Island**

St Helena (15 58`S 5 43`W, Figure 1) lies 1300 km south-east of the nearest land, Ascension Island, and 1800 km west from the nearest continent; meeting Africa at the Angolan coast. It was formed by volcanic activity 14 million years ago, and this has resulted in a landscape of soaring cliffs, steep valleys and little flat land. The island is 17 km by 10 km and covers an area of 121.7 km<sup>2</sup>. The result of this age and isolation has been a plethora of endemic flora and fauna, for example 12 endemic genera of spider have been described (Ashmole and Ashmole 2000). However, no terrestrial mammals or reptiles, or any amphibians are native to the island. St Helena was discovered by a Portuguese sailor João de Nova Castella in 1502, and records suggest that the island was extensively forested at this time. St Helena was used as a stopping point for ships going to and from Europe and Asia for the next two hundred years. Goats and pigs were left on the island to provide food for the sailors, leading to a marked change in the habitat through suppression of regeneration of the native flora.

The rate of this habitat change was steadily increased by a permanent settlement on the island from 1659, and by the time Darwin visited the island in 1836 caused him to comment:

“In St. Helena there is reason to believe that the naturalised plants and animals have nearly or quite exterminated many native productions. He who admits the doctrine of the creation of each separate species, will have to admit, that a sufficient number of the best adapted plants and animals have not been created on oceanic islands, for man has intentionally stocked them from various sources far more fully and perfectly than has nature” (Darwin, *Origin of Species*, in Wilson 2006).

Permanent settlement coincided with a major influx of many invasive mammal species including cats *Felis catus*, dogs *Canis lupus familiaris*, Brown Rats *Rattus rattus* and mice *Mus musculus*, with Norwegian Rats *R. norvegicus*, though it is likely that rodents had been present on the island from shortly after its initial discovery. Common Myna *Acridotheres tristis* arrived later in the 1800's. Today the habitats on the island are largely anthropogenic (Cronk 1989), and related to elevation, from semi-desert (sl-250 msl) and scrub (200-400 msl), to pasture, woodland and extensive areas of New Zealand flax *Phormium tenax* (400-700 msl). The very highest areas are covered by the remnants of the native forest (700-820 msl). The first two categories represent approximately 75 % of the land surface (Ashmole and Ashmole 2000).

The repercussions of human arrival on St Helena have been great for the native flora and fauna, with many species becoming extinct or extremely rare. For instance only two of the 20 known endemic species of land snail are thought still to persist, and several endemic tree species are known from only a few mature individuals; Bastard Gumwood *Commidendrum rotundifolium*, Boxwood *Mellissia begoniifolia*, St Helena Redwood *Trochetiopsis erythroxylon* (Ashmole and Ashmole 2000). The avifauna of St Helena has also suffered; with the extirpation of three endemic and several more widespread seabird species, the restriction of the remaining seabirds to offshore stacks and the extinction of all but one of the six known endemic land birds (Olson 1975). Two of these extinctions, however, are likely to have occurred prior to 1502.

Conservation work is underway on St Helena, notably for the very rare tree species mentioned previously (Ashmole and Ashmole 2000; Fowler 2004). Additionally, much of the island has been designated as Important Bird Areas for the Red-billed Tropicbird *Phaethon aethereus* and the St. Helena Plover *Charadrius sanctaehelenae* (BirdLife International 2011b). St Helena, however, lacks the resources to adequately protect its biodiversity. The island has a small local human population, and is one of only three Overseas Territories still reliant upon the UK for financial aid (Anon 2011).

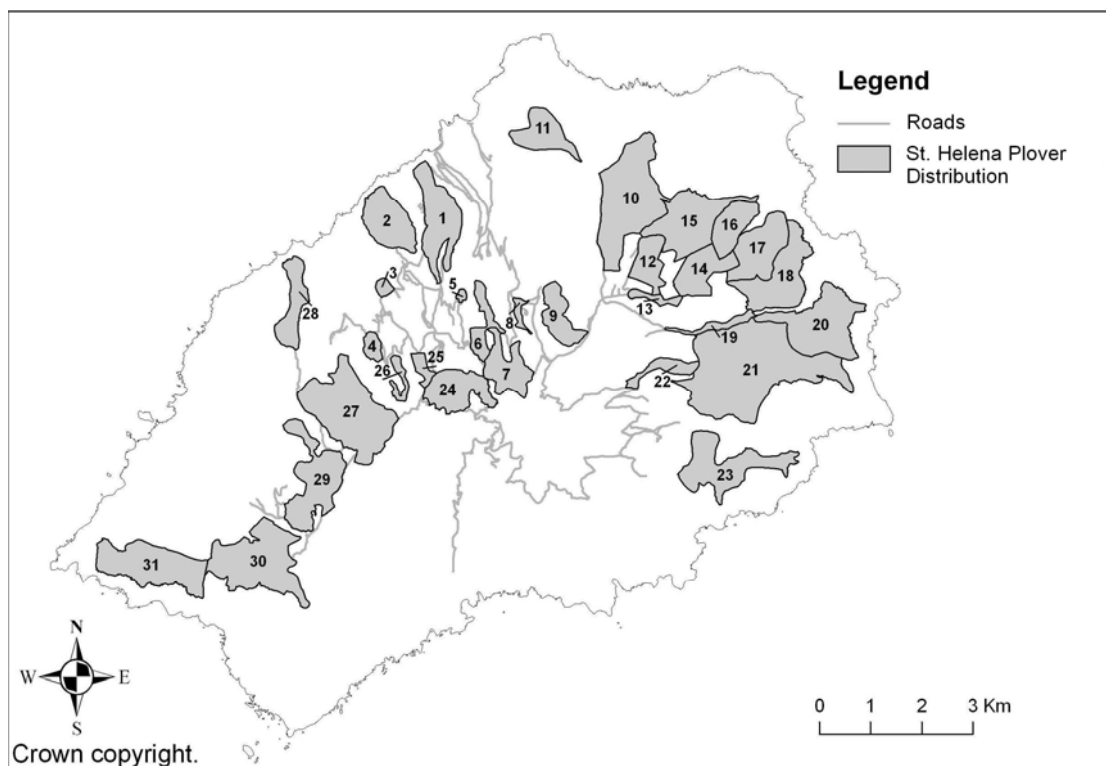
### **St. Helena Plover**

Fossil bones of the St. Helena Plover (also known as the Wirebird, *Charadrius sanctaehelenae*) have been found on St Helena, indicating that it arrived on the island at least several thousand years ago (Ashmole and Ashmole 2000). It is thought that ancestral birds arrived from Africa. Kittlitz's Plover *Charadrius pecuarius* has an extensive range within the drier parts of Africa and is currently acknowledged as the St Helena Plover's closest relative, although as yet there is no phylogenetic evidence for this relationship. The St. Helena Plover was first recorded in 1638 and formally described by Harting (1873). Early population estimates varied widely and were qualitative ("scarce without being rare" (1924), "relatively common" (1960), (Rowlands et al. 1998)), therefore there is little known about natural variations in population size. Although Pitman (1965) addressed some aspects of the plover's breeding biology; with a focus on clarifying the species' taxonomy, it was not until 1988 that an in-depth study was carried out into the species' biology and a direct census over the 31 known St. Helena Plover sites was carried out, the latter giving a mean count of 466 adults (Figure 2, McCulloch 1991).

Within the plovers the conservation status of nine out of 31 species of the genus *Charadrius* are classified as 'Near Threatened' or worse in the IUCN Red List (IUCN 2010). Of these threatened species, the St. Helena Plover has the highest level of threat, Critically Endangered. There has been a decline in St. Helena Plover numbers since the onset of formal studies in the late 1980's (McCulloch and Norris 2001), and a subsequent drop in numbers of 43 % between 2000 and 2005 (McCulloch 2009). However, more recent censuses indicate that the population has stabilized (SHNT 2011).

Of the habitats present on St Helena today the St. Helena Plovers use both semi-desert and pasture. At present around 70 % of the global population breeds on managed pasture land (McCulloch and Norris 2002). In addition to historic habitat modification there has been recent change, in particular on pasture areas. Agriculture production in general has declined, as have livestock densities, which has led to scrub encroachment and an increase in overall vegetation height through reduced grazing pressure (McCulloch and Norris 2002). Habitat surveys have found that St. Helena Plovers breed at highest density on dry pastureland with intermediate levels of rainfall (300-500 mm) and slopes of less than 6 %. This may be partly explained by food availability, St. Helena Plovers are insectivores and pasture areas have higher concentrations of invertebrate prey throughout the year (McCulloch 1992). McCulloch & Norris (2001) also found a negative association with sward height in pasture, with St. Helena Plovers preferring a mean vegetation height less than 10 cm. Habitat associations in the semi-desert however are less clear (McCulloch 2009).

Adult St. Helena Plovers are monogamous and highly territorial; they are ground nesting and may breed throughout the year. They create a small scrape filled with dry vegetation, which is used to cover the eggs when the parent leaves the nest (McCulloch 1992). The demography of the St. Helena Plover is not well understood. Previous studies have estimated nest and brood survival for one site only, Deadwood Plain, and little is known of adult survival rate (McCulloch and Norris 2002).



**Figure 2** - Map of St Helena showing St. Helena Plover census areas (numbered). Key: 1, Cow Path/High Knoll; 2, Donkey Plain; 3, Cleugh's Plain; 4, Rosemary Plain; 5, Francis Plain; 6, Barren Hill; 7, The Dungeon; 8, Prospect Pastures; 9, Sane Valley; 10, Deadwood Plain; 11, Banks' Ridge; 12, Longwood Farm; 13, Longwood Golf Course; 14, Bottom Woods; 15, Longwood Erosion Zone; 16, Weather Station Ridge; 17, Horse Point Plain; 18, Prosperous Bay, North; 19, Fisher's Valley; 20, Prosperous Bay Plain; 21, Upper Prosperous Bay; 22, Woody Ridge; 23, Stone Top Ridge; 24, Central Pastures; 25, Pounceys; 26, Oaklands Pastures; 27, Broad Bottom; 28 Horse Pasture; 29, Blue Hill/Head O'Wain; 30, Southern Pastures; 31, Man and Horse. Names follow the nomenclature of McCulloch (1991).

## **Outline of PhD project**

This project was initiated following the dramatic decline in the population numbers of St. Helena Plover between 2000 and 2005 with the overall aim of understanding the underlying cause(s) of the decline. My PhD had three objectives: to understand the current status of the St. Helena Plover, to investigate aspects of its environment that may threaten its persistence, and to compare conservation options.

Much of our work relied upon individual identification of the plovers. When working with endangered species it is of particular importance to use the most appropriate marking method. We therefore conducted a small trial comparing the utility of colour rings and leg flags (Chapter 1). As the population was no longer declining rapidly when I began fieldwork I instead sought to understand the links between the environment and demography by investigating geographical variation in both. I focused on two aspects of the environment, predator abundance (Chapter 2) and habitat composition (Chapter 3, Chapter 4). St. Helena Plovers are monomorphic and therefore previous studies have assumed males and females to respond similarly to the environment. However, there may be marked difference in the ecology of each sex, knowledge of which may be pertinent to conservation management. I collected DNA samples and used molecular techniques to investigate these possibilities (Chapter 4).

Whilst conservation recommendations were being assessed we wanted to put in place some interim conservation measures to prevent the population declining further. Initial work indicated that nest survival was low, and we therefore trialed the use of nest exclosures to increase this parameter (Chapter 5).

The ultimate goal of my PhD was to investigate the influence of different conservation management strategies on the population, and thus advise future conservation projects. In order to accomplish this I developed an individual based population model using the empirical estimates of demographic parameters and their associations with environmental variables (Chapter 6).



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## **Chapter 1: Leg flags versus colour rings: a comparison of marking methods using a small shorebird, the St Helena Plover**

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**N.B. In the published version of this manuscript the species is referred to as the St Helena Wirebird, or Wirebird.**

### *Author's contributions*

FB: Data collection, statistical analysis, manuscript preparation

TS: Statistical advice, manuscript improvement

MB: Study design, manuscript improvement

## Abstract

To understand the behaviour, life-history and demography of animals it is often necessary to mark individuals in some way to tell them apart from conspecifics. It is important to choose the most effective method of doing this as it will allow the number of study animals to be minimized. Plastic colour rings have been used to mark birds for many years, and more recently, leg flags engraved with numbers or letters have become available. Engraved leg flags may have some advantages over colour rings; however, we are not aware of any comparison of the effectiveness of these two techniques. As part of a conservation-focused demography project, St. Helena Plovers, *Charadrius sanctaehelenae*, were either marked with one leg flag or three colour rings and the ease of resighting was investigated in the natural habitat of the plovers. Results showed that there was a lower probability of correctly identifying the engraved numbers on the leg flag than the combination of colour rings, when controlling for confounding factors. Both the distance from the subject to the observer and the duration of the trial reduced the probability of correct identification. Although these results may differ between species and habitats, it is anticipated that they will help researchers to select appropriate marking techniques.

## Introduction

Individual identification has allowed scientists to understand much more about the ecology, movements and behaviour of animals, (Clark *et al.* 2009; Kosztolányi and Székely 2002b; Teunissen *et al.* 2008) and it has also helped to refine estimates of population size, survival and productivity (Calvert and Robertson 2002; Sandercock *et al.* 2005a; Spear and Nur 1994). Some identification techniques have minimal impact on the subject animals; for example remotely observing natural variation in phenotype (Langtimm *et al.* 2004). However, the majority of identification techniques involve capturing the animals on one or more occasions, and these techniques therefore have the potential to negatively affect animals both from the capture process and from the mark itself (Amat 2006; Sharpe *et al.* 2009). Thus, it is beneficial to use the most effective marking technique, in order to maximize data collection for a given number of marked individuals. Effectiveness is defined here as the ability to accurately and quickly identify a marked individual.

Colour rings began to be used as a technique to mark birds around 50 years ago. Applying one or more colour rings to a bird means that they can be identified remotely at a group or individual level, and therefore the need for recapture is reduced. Compared to traditional metal rings, colour rings can decrease the time required to estimate adult survival and increase the accuracy of these estimates (Brochard *et al.* 2002). Leg flags are very similar to colour rings, but have a small flap of plastic that extends from the ring (Fig. 1). Leg flags were first used in the 1970s as a way to detect a marked bird from a greater distance (Clark 1979) and are often used with an assigned colour scheme as a country or area code for migrating shorebirds. Leg flags were first engraved with letters and numbers in 2000 (Clark *et al.* 2005) and so can now be used as a unique identifier. Large colour rings have also been engraved with letters and used successfully on large shorebirds and waterfowl. Leg flags are an attractive alternative to colour rings in some respects. For example, since unique identification can be achieved using only one colour mark, handling time will be reduced. As the effectiveness of leg flags as a unique identifier has not been investigated to date, this study seeks to compare the relative effectiveness of colour rings and colour flags, using the St. Helena Plover *Charadrius sanctaehelenae* (also known as the Wirebird) as a study species.

## Methods

### *Study Area and Study Species*

The St. Helena Plover is a small sandplover endemic to St Helena Island in the Atlantic Ocean (15°58'S, 5°43'W). It is designated as Critically Endangered (BirdLife International 2007) due a population decline to 208 adults in 2005 (McCulloch 2009). The St. Helena Plover is relatively tolerant to human presence, and, although there was variation in this trait, most birds could be approached to within 30 m by an observer on foot. Study sites across the island were used, exhibiting a range of climatic and habitat characteristics. The dominant habitat type was dry pastureland. Areas of semi-desert were also used by the plovers (McCulloch 1991; McCulloch and Norris 2001).

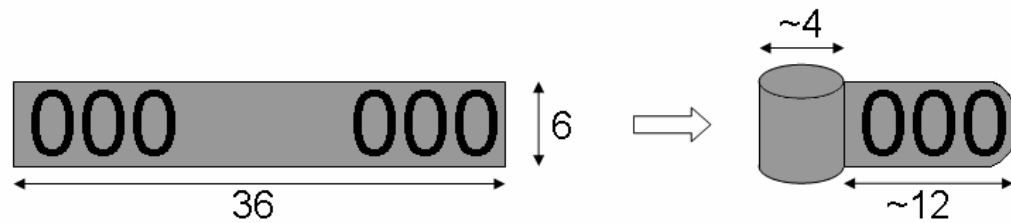
### *Study Design*

Adult St. Helena Plovers were caught at the nest using either a walk-in funnel trap (Székely et al. 2007a) or a Potter trap, modified after Bub (1978). All individuals were fitted with a metal, incoloy, British Trust for Ornithology (BTO) ring (internal diameter 3.3 mm, height 5.5 mm) on the left tarsus, and with either an orange leg flag engraved with three numbers in black ink (on the tibia), or three butted colour rings (one on each tibia, and one on the right tarsus). Fig. 1 shows the dimensions of the flags, which were prepared following guidance in Clark (2005). The numbers on the flag were each about 4 x 3 mm. The butted colour rings had an internal diameter of 3.3 mm and height of 4.5 mm. The colours of rings used were: white, yellow, orange, red, light green (lime), green and royal blue. Solvent cement (Marley ®) was used to secure both the colour rings and the leg flags. Our starting methodology was to alternate between marking methods for successive birds. However, as some leg flagged birds were observed pulling at their flag with their beaks several weeks after application, and as the species is endangered, it was decided to halt the application of the flags. This led to an imbalance in the study design that was addressed by sampling each individual on more than one occasion and dealing with the resulting pseudoreplication in the data analysis. Chicks were given a metal ring at hatching and were uniquely colour marked at around two weeks of age, using the same methods as outlined above. A few chicks evaded recapture and so fledged with only a metal ring. Trapping and ringing were carried out



from 21 November 2007 to 27 February 2008. Resighting for the trial was also carried out during this period.

During visits to each site marked individuals were sought and an attempt made to read their code. Each trial was given a binomial response, (1, 0) for success and failure respectively. A trial was only coded as a success if the entire combination of rings, or all three numbers on the flag, were correctly identified. A code was deemed to be correct if it had been used. The distance from the observer to the bird was recorded (in paces). If it was not possible to read the code then the distance was taken as the closest point that the observer got to the bird during the trial. The duration of each trial was recorded, as was the time of day the trial was undertaken. Habitat characteristics and bird activity were recorded as rank variables. Habitat code levels were scored as bare ground, short (pasture) vegetation, medium (scrub) vegetation, whereas activity code levels were scored as stationary, walking, running.



**Fig. 1** - Schematic showing dimensions of the leg flags (mm) before and after manufacture.

Field work was carried out on foot using x 8 binoculars by a single observer (FB). This trial used binoculars, rather than a telescope, due to field constraints. Any loss of colour rings or flags was investigated using data obtained during a second field season from 6 November 2008 to 27 February 2009.

#### *Data Analysis*

A Pearson's Chi-squared test with Yates' continuity correction was used to investigate whether the proportion of trials that were successful differed between the two test groups; leg flags and colour rings. A Generalized Linear Mixed Model (GLMM) was used to account for the pseudoreplication resulting from individual birds being the subject of more than one trial; this used a binomial response, and the logit link.

Individual identity (Bird\_ID) was used as the random factor and all other variables fixed effects. Trial duration, time of day and the distance between the bird and the observer were continuous variables; and mark type, activity code and habitat code were factors. In order to include Bird\_ID as a random factor it was essential to know the identity of the bird. This was simple for successful trials; however it was less straightforward for trials where the observer had not managed to read the combination. Fortunately, for many of this latter group of trials it was possible to infer the identity due to territoriality. The vast majority of birds are territorial, and therefore any influence on the success of reading the code due to prior knowledge would be equal amongst individuals. The small number of trials (eight) where it was not possible to identify the bird unambiguously were removed from the dataset for this analysis. The GLMM was first investigated with the main effect of mark type and the random factor of Bird\_ID only. The variance accountable to this random term was so small that it was considered satisfactory to use a Generalized Linear Model (GLM). Initially a maximum model was tested using all factors and continuous variables, and all the interactions up to second order that were judged to be biologically meaningful. The minimum adequate model (MAM) was calculated by deleting non-significant terms until those remaining were all significant at least at the 95% level. Program R (R Core Development Team 2004) was used for all statistical analysis.

## **Results**

51 adult St. Helena Plovers (43 with colour rings; 8 with leg flags) and 12 chicks (11 colour rings; 1 leg flag) were individually marked. Thirty-one marked individuals were re-sighted during the study period, some on several occasions, giving a total of 74 resightings. Forty (74%) of the colour ringed birds were re-sighted one year after ringing and only one bird had lost one ring. This gives a rate of loss of  $0.83\% \text{ yr}^{-1}$ . Seven (78%) of the flagged birds were re-sighted after one year and all still had their flag. If a bird had lost its flag it would retain a metal ring and several birds were seen at least a year after ringing with only a metal ring. However, it was not possible to unambiguously detect flag loss as these birds could also have been one year old birds that had evaded recapture for colour ringing as chicks. No leg injuries were observed on any colour marked bird. During the re-sighting period there was no observed fading or discolouration of colour rings or flags.

**Table 1** - *Generalized Linear Mixed Model in which the response variable was trial success using a binomial error structure and logit link – for all trials where Bird\_ID was known or inferred.*

Fixed Effect $N$ (66)				
Variable	$\beta$	T	P	AIC
Marking method (flag)	-3.63	-5.011	<0.0001	195.30
Random Effect ( $N = 66$ , groups: 31)				
Variable	Variance		Std Dev	
Bird_ID	$1.031 \times 10^{-10}$		$1.016 \times 10^{-5}$	

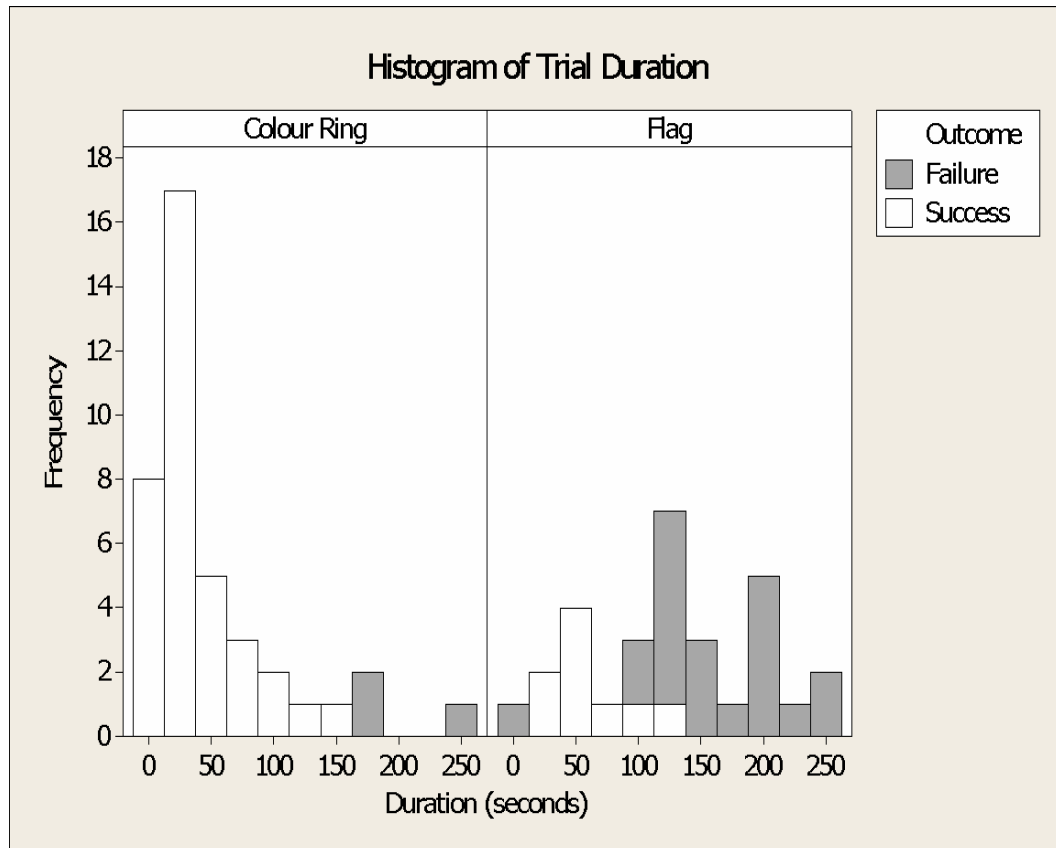
Figures given correspond to the partial slope ( $\beta$ ), the t-score, the P-value associated with that t-score and AIC (Akaike's Information Criterion) or penalized log-likelihood. This latter term is a measure of the suitability of a model given the model fit and the number of estimated parameters.

Successful reading was more likely with colour rings than with leg-flags, 36 out of 43 compared to 5 out of 31 ( $\chi^2_1 = 30.62$ ,  $P < 0.0001$ ). The results of the GLMM (Table 1) also show a highly significant association between success and mark type ( $t_{64} = -5.01$ ,  $P < 0.0001$ ). The variation accounted for by the random effect (Bird\_ID) and its associated standard deviation are very small. Due to the sample size it is not possible to fit all the explanatory variables into the GLMM at once. The MAM (Table 2) shows the same strong association between low identification success and mark type (flag) when other explanatory variables are included. Additionally, there is a significant negative association between success and both distance and duration.

**Table 2** - *Generalized Linear Model in which the response variable was trial success, with binomial error structure and logit link. See justification in the text.*

Explanatory Variable	$B$	$Z$	$P$	AIC
Minimum Adequate Model $N$ (74)				
Marking method (flag)	-3.53	-3.19	0.0014	41.40
Distance	-0.13	-2.56	0.010	
Duration	-0.032	-3.18	0.0015	

Figures given correspond to the partial slope ( $\beta$ ), the z-score, the P-value associated with that z-score and AIC (Akaike's Information Criterion) or penalized log-likelihood.



**Fig. 2** - Frequency histogram of trial duration, illustrating that both successful trials and colour ring trials tend to have a shorter duration than unsuccessful or flag trials.

## Discussion

The results obtained from this study show that, for this species and research methodology, a combination of colour rings can be read successfully more easily than the numbers on a leg flag. This result holds when environmental variables and individual variation are taken into consideration. Despite the difficulty in identifying the code engraved on the flags it was observed that the flags are more conspicuous than the colour rings as the presence of a flag could be detected from a greater distance. Clark (1979) found that the presence of a colour flag could be detected from a distance of up to 600 m using a telescope. Leg flags were first designed for this purpose, Brochard (2002) used one leg flag along with four colour rings and found that the flag was a good way to initially identify that a bird was colour ringed.

The MAM showed a negative association of success with the explanatory variables trial duration and distance from the observer to the subject. This is as predicted for distance, as the distance between the observer and the subject decreases, the probability of successfully identifying the bird increases. However, it appears to be counter-intuitive for trial duration; as trial duration increases the frequency of success decreases (Fig. 2). What this trend does show is that the higher occurrence of successful trials for colour rings was not due to these trials lasting longer. The negative association between trial duration and success can be explained by the fact that the easier a combination is to read, the shorter will be the time taken. Conversely, if reading the combination is proving difficult the trial will last longer and is more likely to be unsuccessful. An interaction term was included in the maximum model for trial duration and mark type (in the GLM); however, this term was not retained in the MAM.

Use of binoculars in this study rather than a telescope may have affected the proportion of colour marks that could be read. Telescopes are often used to observe waders, however, since it is possible to get much closer to St. Helena Plovers than most other wader species the effect of using lower magnification optics would be reduced. In this study the birds were widely spaced and observed individually. However, when looking for marked birds in a flock it may be better to have a single unique identifier rather than multiple colour rings, as determining which legs belong to which bird becomes challenging in this situation (e.g. Gillings *et al.* 2009).

It is possible that flags can be read more easily depending on the combination of background and engraving colour used. However, a recent paper looking at engraved colour rings found no significant difference between any of the colour combinations tested (Mitchell and Trinder 2008), which included the one used in our experiment: black writing on an orange background. Therefore it is not anticipated that different flag or engraving colours would substantially affect the outcome of our trial. The St. Helena Plover is one of the smallest species that engraved leg flags have been used on, and it is possible that leg flags are more suitable for bigger species where the size of the lettering can be larger. By using fewer digits, the size of the lettering on our flags could have been widened, but it could not have been increased in height without bringing the size of the flags outwith the recommendations of the BTO (Redfern and Clark 2001).

There are other factors to consider, apart from readability, when comparing these two marking methods, including handling time, mark retention and any variation in the impact the mark has on the behaviour or vital rates of the bird. Leg flags have the advantage that only one has to be applied to uniquely mark individuals. This can save handling time, thereby reducing the stress to the bird. Leg flags also may be advantageous for birds with short legs that cannot be fitted with multiple colour rings. Moreover flags may be more suitable for large-scale studies because far more unique alphanumeric codes are possible than distinctive colour-ring combinations. From observations made one year after marking, both methods were confirmed to have a high retention rate and neither raised concerns due to observable injuries related to the marking process. The rate of predation on adult St. Helena Plovers and their chicks is not yet known. It is believed to be relatively low for adults, but could be considerable for chicks. Therefore, highly conspicuous, brightly coloured leg flags and colour rings could impact survival by making them more conspicuous to predators, although this is likely to depend on the colours used and the habitat that the birds are in. There are no published studies known to the authors of the effect, if any, of leg flags on the behaviour or vital rates of birds. From casual observation it was seen that some birds continued to pull at the leg flag for several months after marking. It is unlikely that they would be able to remove the flag but they are clearly aware of it. Flags could also have negative impacts on the energetics of locomotion, in particular for chicks in long vegetation. Finally, some colours of colour rings have been shown to influence social interaction in a variety of species (Burley et al. 1982; Wheeler and Lewis 1972 cited in Calvo and Furness 1992) and it is possible that leg flags will have a similar impact.

The results of this study show that for this species and this research protocol colour rings are to be preferred over engraved leg flags. This preference could be different for other species and research methods, for example, if the size of bird allows larger flags to be used. This paper serves to give researchers some of the information they need to decide which marking method is the most suitable for their proposed study. There have been several reviews of marking methods for birds, the most recent being undertaken 18 years ago (Calvo and Furness 1992). An updated review would be beneficial to the research community.

## Acknowledgments

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## **Chapter 2: The impact of introduced predators on an island endemic, the St. Helena Plover *Charadrius sanctaehelenae***

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TS: Manuscript improvement

MB: Manuscript improvement

## Abstract

Predation is an important driver of species' ecology and its observed influence is a balance between the evolutionary adaptations of both predator and prey. However, this balance can break down if species are introduced outside of their natural range. Here we investigate the impact of introduced predators on the productivity of the St. Helena Plover *Charadrius sanctaehelenae*, endemic to the South Atlantic island of St Helena. Nest predator species identified have all been introduced to St Helena and are all amongst those species known to be invasive on other islands. The species responsible for taking the largest proportion of eggs was the domestic cat *Felis catus*, with rats *Rattus rattus* or *R. norvegicus* and Common Myna *Acridotheres tristis* taking smaller proportions. Nest survival varied spatially and was correlated with an index of cat density. However, no relationship was observed in the number of nesting attempts per pair in a year, indicating that this was limited, most likely by food availability, but potentially also by the non-lethal influence of predators. Given estimated values of other demographic parameters it is likely that productivity is insufficient in some areas to allow stable populations locally; this is largely attributable to variation in nest survival. Future work should target assessing the population level impacts of current and reduced predator densities, and understanding the influence of resource availability and habitat structure in mediating the impact of predators.

## Introduction

Predation is a ubiquitous feature of life for many species, and an important determinant of species distributions and population dynamics. Although detrimental for the individual, predation can serve to both stabilise populations and to increase prey species diversity (Newton 1998; Paine 1966). Previous investigations of predation focussed on the consumptive effects of predation; recently, however, the importance of non-lethal predator effects in controlling prey behaviour, morphology and spatial distribution has been highlighted (Beckerman et al. 2007; Cresswell 2008; Preisser et al. 2005). Recording high levels of predation, however, is insufficient to show that predators are limiting prey populations (Lima 2009); limiting factors either cause a population to decline or prevent it from increasing (Newton 1998). The proportion of mortality attributable to predation may vary inversely with the proportion attributable to other causes, for example disease and starvation, resulting in little or no influence on total mortality. In this way predation may not add to overall mortality but be seen to be compensatory (Errington 1956).

Predation may act on all prey life stages. Predation on young and inexperienced animals is, however, often severe. In most bird species for example predation is the main cause of nest or brood failure (Newton 1998; Ricklefs 1969). Nevertheless, individuals may compensate for high levels of predation on their offspring by having multiple breeding attempts in a season. Carefully designed experiments are the best way to find out if predation is limiting a species. Different areas or times across which predator densities vary can also be compared (Gibbons et al. 2007).

In general predation rates represent a balance between the evolutionary adaptations of predator and prey (Ricklefs 1969). The absence of a shared history can therefore leave prey species poorly adapted to cope with predators. This is often the case for prey species endemic to isolated oceanic islands, whose native faunae are disharmonic and commonly lack certain groups, notably predacious mammals (Gillespie and Clague 2009). Therefore, although introductions have not been more frequent on islands, island species are often more severely impacted (Clavero and García-Berthou 2005; Hilton and Cuthbert 2010). For example, eighty percent of bird extinctions since 1600 were from islands (Johnson and Stattersfield 1990). The probability that a bird species has been

lost also correlates with the number of different predators species introduced since European colonisation (Blackburn et al. 2004). The absence of certain predator guilds partly explains the differences in the characteristics of island species compared to their mainland relatives; for example size change, loss of dispersal ability, loss of defensive adaptations and reproductive change; for instance laying fewer but larger eggs (Clegg and Owens 2002; Whittaker and Fernández-Palacios 2007; Williamson 1981). As awareness of these substantial negative impacts of introduced predators has grown, attempts to control or eradicate them from islands have recently increased both in number and scale (Brooke et al. 2007; Hilton and Cuthbert 2010; Nogales et al. 2004). Controlling animal populations raises ethical questions and can provoke public concern. It may also lead to unexpected numerical or behavioural responses in prey or mesopredator species (Bergstrom et al. 2009; Murphy and Bradfield 1992; Ritchie and Johnson 2009). The influence of introduced predators, both on the target species and the wider ecosystem, must therefore be investigated prior to any management. This study reports on efforts to accomplish this for an endangered bird species, the St. Helena Plover *Charadrius sanctaehelenae*.

The St. Helena Plover (Critically Endangered, BirdLife International 2009; McCulloch 2009) is endemic to the island of St Helena (15 58'S 5 43'W) in the South Atlantic Ocean. The endemic birds of St Helena conform to the general pattern of island life described above, and sadly all those species present at the islands discovery by humans in 1502 have since become extinct, except the plover (Olson 1975). St Helena had no native mammal species and these extinctions were surely influenced by the many predatory mammal species introduced to the island after its discovery, including cats *Felis catus*, dogs *Canis lupus familiaris*, rats *Rattus rattus* and *R. norvegicus* and mice *Mus musculus* (Ashmole and Ashmole 2000). The Common Myna *Acridotheres tristis* (Rowlands et al. 1998) was also introduced and is a potential predator of eggs and small chicks. Given the severe impacts of introduced predators elsewhere we might expect the plovers to be similarly influenced, and high levels of predation are a possible reason for the current small population size. The plovers have, however, persisted in the presence of introduced predators for hundreds of years and so the effects of predation remain unclear.

The adult survival of the St. Helena Plovers is high (Burns 2011, Chapter 4), and therefore predation is likely to be primarily influencing productivity. The plovers breed throughout the year, however (McCulloch and Norris 2001), and therefore may re-nest on multiple occasions both following failure and success. Other tropical species have been shown to be able to compensate for high nest predation in this way (Roper 2005). Furthermore, St. Helena Plovers have a small clutch size which is often seen as an adaptation to high nest predation, as it may allow more energy to be saved for future nesting attempts during the season (Farnsworth and Simons 2001; Martin 1995).

In order to investigate the current influence of predators on the productivity of the St. Helena Plover the following questions were posed:

1. What proportion of nest failure can we ascribe to predation and which species are involved?
2. Does variation in the relative density of any predator species predict variation in nest survival?
3. Does the number of nesting attempts year<sup>-1</sup> pair<sup>-1</sup> vary with nest survival?

## **Methods**

### *Nest survival and re-nesting*

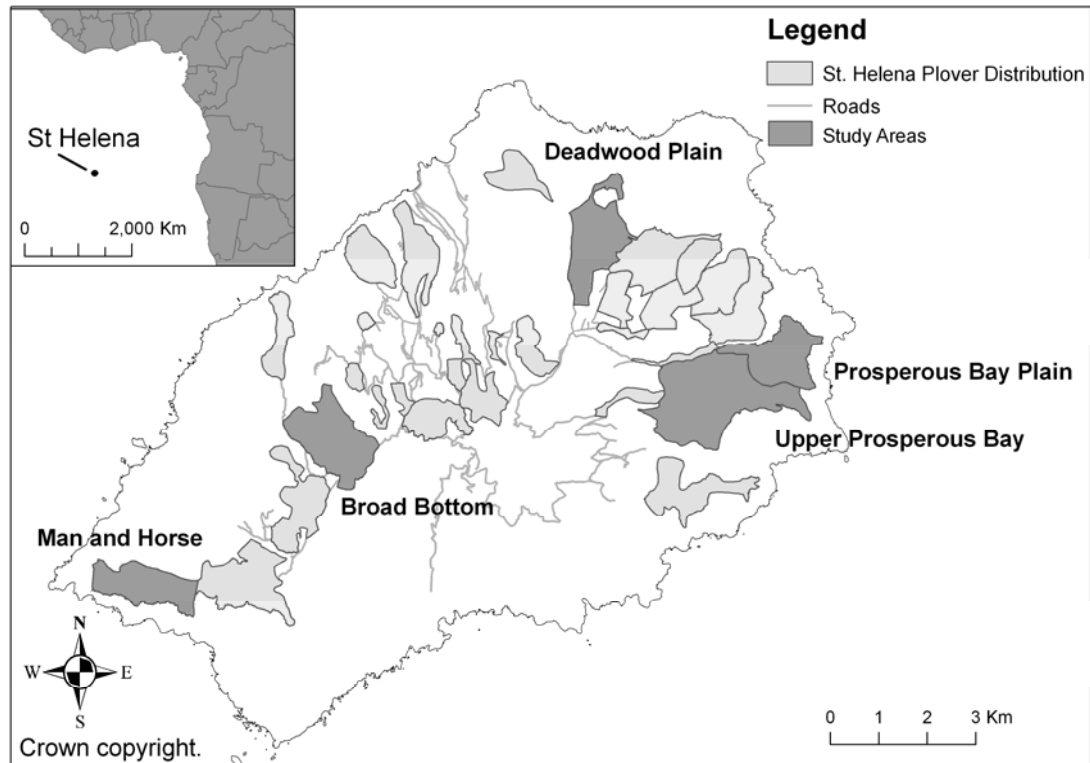
Data were collected between November 2007 and February 2010 in the field; the period over which data were collected is given below for each analysis. Five study sites were used, encompassing roughly half of the global plover population (Deadwood Plain, Broad Bottom, Man and Horse and Upper Prosperous Bay and Prosperous Bay Plain, Figure 1). The sites are dispersed across the island and were selected to encompass the range of habitat types and environmental conditions experienced by the plovers; the first three sites are pasture and the latter two semi-desert. Few birds were followed at Prosperous Bay Plain, and as the two semi-desert sites are contiguous, data from them were pooled and referred to as Prosperous Bay.

Nest survival data were collected throughout the core breeding season from November to February in 2007 and 2008. Each nest was visited approximately every five days up until a few days before it was predicted to hatch, at which point nests were checked at least every second day. Nests were checked from a distance where possible, to avoid

disturbing the incubating bird. Nests were classified as successful if chicks were seen with a colour ringed parent, or chicks of an appropriate age seen close to the nest scrape. The nest was deemed to have failed if the scrape was found empty and parent birds were in the area but not exhibiting any behaviour typical of adults with young chicks. If the parent birds could not be seen within ~ 100 m of the nest then it was classified as failed, as parents with very small chicks are unlikely to move far within the first day after hatching. In order to investigate the role of predation in nest failure we classified the cause of each failure. When eggs were absent they were classified as predated, eggs were assumed infertile if they failed to hatch when incubated to term, and abandoned if left unattended for over 24 hours. Previous authors have used the presence of small shell fragments in the scrape to indicate hatching, however, as shell fragments were not always present in successful nests we chose not to use this criterion. A sample of pairs at each site (N = 6-10) were followed for a 12 month period, from April 2008 to March 2009, in order to assess annual productivity and re-nesting rates. At least one bird in these pairs was colour ringed, for full details of the colour ringing protocol see Burns et al. (2010).

#### *Nest predators*

Throughout the same period as that for nest survival, nest cameras were installed at a sample of nests; additionally one nest was monitored in February 2010. The detailed design of the cameras was described in Bolton et al. (2007). In brief these small motion sensitive cameras (2.5 cm diameter) were mounted on stakes ~ 50 cm from the nest at a height of ~ 25 cm. The cameras have an infrared array allowing filming in darkness. All other components of the camera system were carefully buried under the ground to minimize conspicuousness. Nests with cameras were only disturbed to change the batteries; approximately every five days. The number of nests that were monitored using these cameras was balanced between sites.



**Figure 1 – Map showing the known distribution of the St. Helena Plover, with the location of study sites in darker grey and the location of St. Helena inset.**

#### *Estimating nest predator densities*

The index of cat density was estimated by calculating the deposition rate of scat along a five kilometre transect at each site. Transects were conducted four times at each site; approximately monthly between June and October 2009. During the transects the location of any cat scat within 2 m of the centreline was recorded, and the scat collected for further analysis. Myna density was estimated using a similar transect approach, between October 2007 and February 2008. A count of Myna birds was undertaken whilst walking a transect of approximately 1 km through each site, any Myna that were seen were counted, regardless of the distance from the transect line. Birds in flight were included in the count. No other activities were undertaken during the transects, and therefore walking speed was assumed constant. The time taken to complete the transect was recorded, and the density of birds expressed as Myna birds second<sup>-1</sup>. This procedure was repeated on each visit to the site, sample sizes are given in Figure 3.



Rat density is commonly estimated using indices of abundance, for instance using tracking tunnels, snap traps or wax blocks. An inherent assumption of these methods is that the index is related to rat density. However variation in home range size, activity, hunger level or neophobia can result in substantial biases (Wilson et al. 2007).

Although comparisons between methods have shown some congruence, results have been mixed (Blackwell et al. 2002; Thomas 1999; Whisson et al. 2005). Therefore, we used two methods, as suggested by Blackwell et al. (2002), so that the robustness of our results would be reinforced if both indices exhibited similar patterns. The two methods used were flavoured wax blocks and oil impregnated chew sticks; both designed to detect bite marks. The wax blocks were prepared following the guidelines in Handford (2004). Thomas (1999) showed that the bite marks of rats on wax blocks could be differentiated from those of other species, such as mice and rabbits due to differences in dentition. Mice produced very small faint marks compared to those of rats, and rabbits could be identified due to the presence of serrations in their incisors. In our study carnivores (cats and dogs) and livestock (cattle and sheep) were also present and could access the sticks and blocks. However, it was possible to identify signs of these species by their size and characteristic carnivore dentition.

The blocks and chew sticks were set out in stations consisting of two of each item. The stations were distributed in transects of ten stations at 50 m intervals, six transects at each of the three pasture sites and eight transects in the semi-desert. The number and location of transects followed advice in Gillies and Williams (2002). Stations were deployed for approximately five days. Transects were replicated twice at each site between June and October 2009. Both methods measured the proportion of objects chewed by rats out of the total deployed, excluding any blocks or sticks found to be missing or damaged. For logistic reasons data estimating the densities of cats and rodents were collected out of the main breeding season of the St. Helena Plover.

### *Analysis*

All statistical analysis was carried out in programme R (R Core Development Team 2004), unless otherwise stated. The site specific estimates of predator densities were compared using ANOVA. Filgner tests and Shapiro tests were used to test equivalence of variance and normality of residuals. If necessary the response variable was transformed. Nest survival was modelled using programme MARK (White and

Burnham 1999). Explanatory variables tested during model selection were: as factors; site, presence of nest camera, and year; as covariates, index of cat density, age of nest and laying date (linear and quadratic). Laying date represents the number of days between the start of the core field season, 5<sup>th</sup> November and the start of laying. The mean number of scat observed transect<sup>-1</sup> was used as an index of cat density. Although a nest specific estimate of the index of cat density would be desirable, for instance the number of scat found within a radius of each nest, an average estimate was used for two reasons. Firstly, due to the small sample size of scat found in some areas, it is unlikely that spatial distribution of scat reflected that of cats. Furthermore, even where sample size was higher, scat deposition is likely to be non-random within a territory and distance from scat is unlikely to be directly related to risk of nest predation on the scale measured. Secondly, only a small proportion of each site, that within 2 m of the transect line, was searched for scat, and therefore the proportion of the transect line within a set radius of each nest, and therefore the area searched, would vary. Rat density and Myna density were not included as explanatory variables; see results for justification. Model selection was based on minimizing AIC.

## Results

### *Nest predators*

The majority, 16 out of 20, recorded nest predation events occurred at night, between 8.30 pm and 4 am, and 65 % of nests were predated by cats (N = 13 nests, Figure 2), most likely including both domestic and feral cats. Camera footage also showed rats and Myna birds taking a smaller proportion of nests. At one nest, an egg at the point of hatching was overcome by ants. From nest visits the chick was known to be alive when the ants entered the egg. However, it is not known whether the chick would have hatched in the absence of ants or whether the ants were attracted by the chick or by other egg contents. The ant species was identified as the big-headed ant *Pheidole megacephala*. This species has been introduced to St Helena and is also the most common ant species on the island (Wetterer et al. 2007). Cattle or sheep are present on the majority of pasture sites in the St. Helena Plover's range. Although livestock occasionally nudged the cameras out of alignment, they did not damage the nests, except during one recording a sheep was filmed taking at least one egg.

### *Estimating nest predator densities*

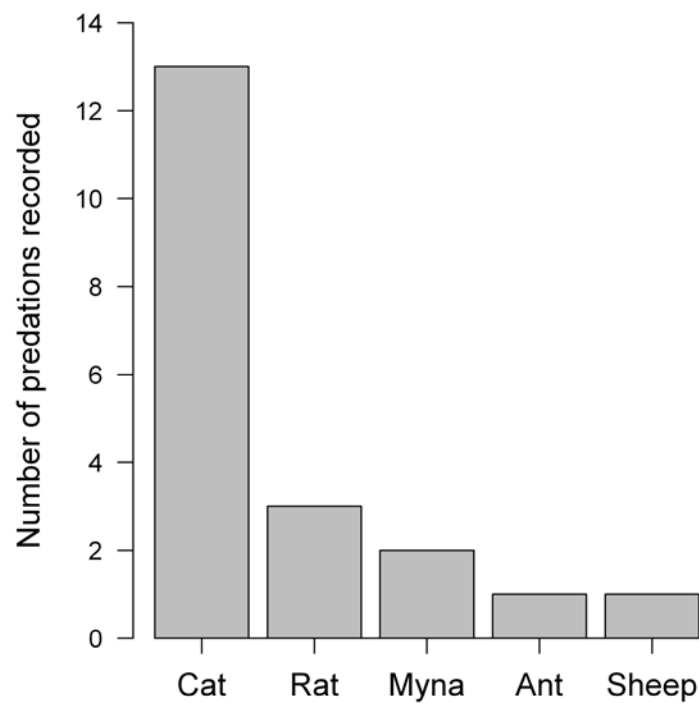
Cat density varied significantly between sites (Figure 3a; Table 1). Comparisons showed that Man and Horse and Prosperous Bay had significantly higher estimates compared to Broad Bottom. The most parsimonious model of Myna density contained two levels of site representing the two habitats present, semi-desert and pasture. Pasture areas had higher densities of Myna birds compared to the desert ( $F_1^{47} = 42.82$   $P = <0.001$ , arcsin transformed; Figure 3b). Figure 4 shows the estimated densities of rats at each site for the two survey methods. There is good congruence between the methods at three of the sites, but nearly complete disagreement at Prosperous Bay; the semi-desert area. Therefore, we analysed data from the three pasture sites only (Table 2). The pasture model showed no interaction between site and survey method, lending support to the results. The index estimated using wax blocks was higher than that found using chew sticks, and there was some indication that rats densities were lower on one site, Deadwood Plain. Since Myna numbers varied only between habitats and we could not be confident of the estimate of rat density in the semi-desert these indices were not used in the analysis of nest survival.

**Table 1** – Results from an ANOVA showing that cat densities, as indicated by the scat deposition rate, are significantly different between the four sites.

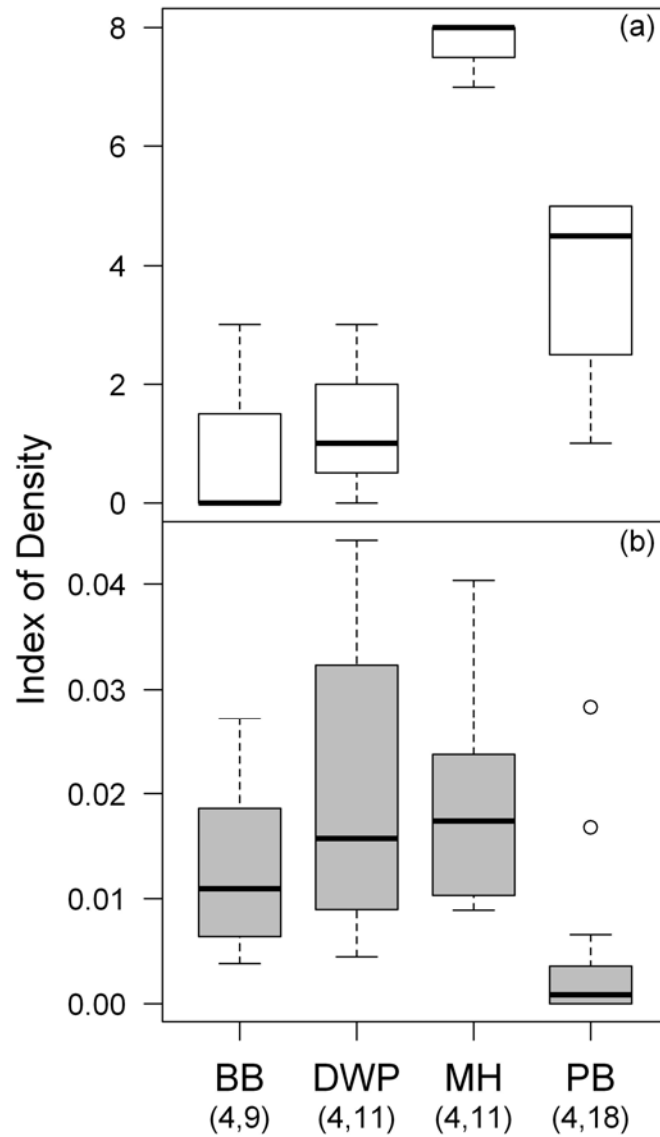
<i>Response – Cat scats transect<sup>-1</sup></i>		Adj. $R^2 = 0.803$ , $F_3^{12} = 21.35$ , $P = < 0.001$		
	Estimate	S.E.	t-value	P
Intercept (Broad Bottom)	0.7500	0.6922	1.083	0.2999
Deadwood Plain	0.5000	0.9789	0.511	0.6188
Man and Horse	7.0000	0.9789	7.151	<0.001 ***
Prosperous Bay	3.0000	0.9789	3.065	0.00982 **

**Table 2** – Results of a Generalized linear mixed model with binomial errors. Response - Proportion of blocks / sticks chewed by rats per transect. Random effect of 1|site/transect.

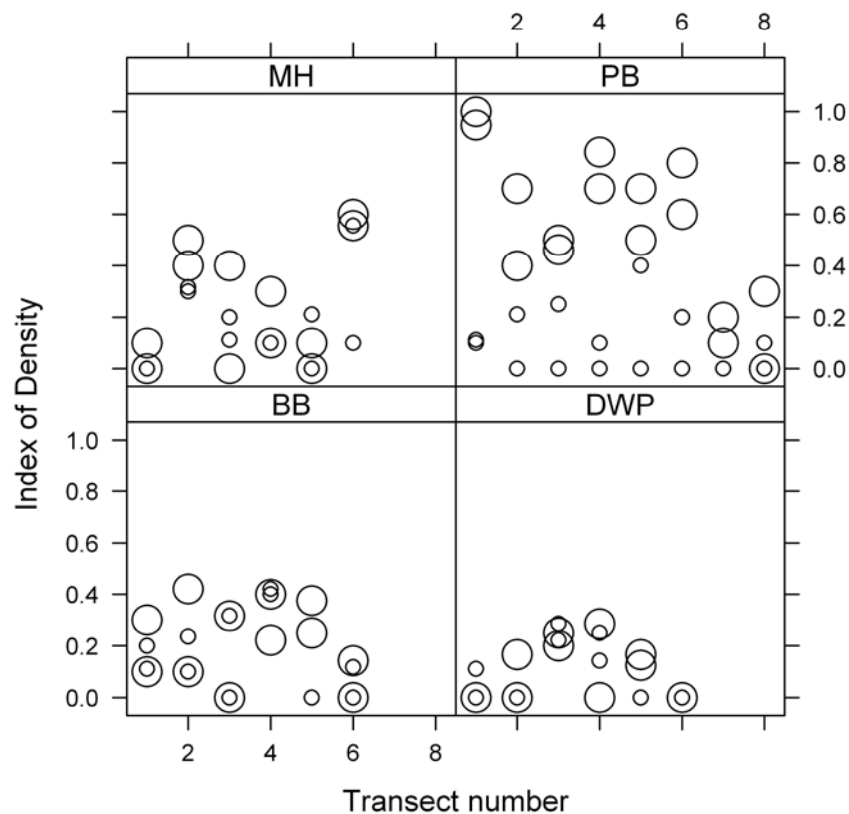
N (Obs: 72, transect 18; site 3)				
Fixed effects	Estimate	S.E	z-value	P
Intercept (Broad Bottom)	-1.70108	0.39579	-4.298	<0.001 ***
Deadwood Plain	-1.12264	0.57570	-1.950	0.0512 .
Man and Horse	-0.06979	0.52981	-0.132	0.8952
Method – Wax Blocks	0.47107	0.22761	2.070	0.0385 *



**Figure 2** – Frequency distribution of predations of St. Helena Plover nests by all recorded predator species



**Figure 3** – Relative densities of nest predators at the four study sites; BB – Broad Bottom, DWP – Deadwood Plain, MH – Man and Horse, PB – Prosperous Bay, (a) cat scat transect<sup>-1</sup> (b) Mynas seen second<sup>1</sup> transect<sup>-1</sup>. Sample size (cat transect, Myna bird transect) is shown in brackets below each site.



**Figure 4** – *The proportion of blocks or sticks per transect chewed by rats at each study site. Small circles are for chew sticks, large circles for wax blocks.*

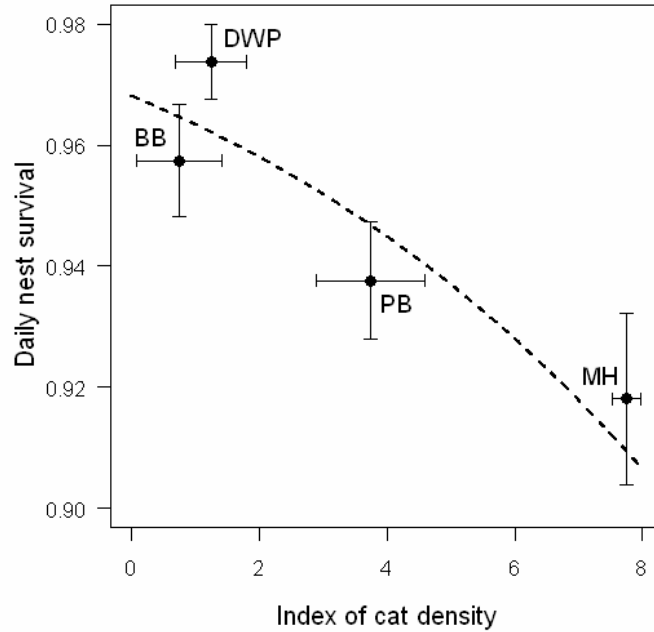
#### *Nest survival and re-nesting*

The total number of plover nests followed over the two years was 173, and of these 65 hatched at least one egg. Predation was by far the greatest cause of nest failure. Including partial predation it was responsible for 93 % of failed nests. A small number of nests were abandoned (4), infertile (6 eggs from 5 nests) or trampled (1). Nests that were abandoned after partial predation were counted as predated. Table 3 shows the output from nest survival analysis in programme MARK. Model 9 demonstrates substantial variation in nest survival between sites. However, the index of cat density explains nearly as much variation as site identity (Table 3, model 10; Figure 5). Since we only have one estimate of cat density for each site we cannot have a model containing both site and cat density as explanatory variables. The only other parameter that explained a substantial proportion of the variation in nest survival is the laying date. The survival of nests appears to decline over the course of the season (Figure 6). There

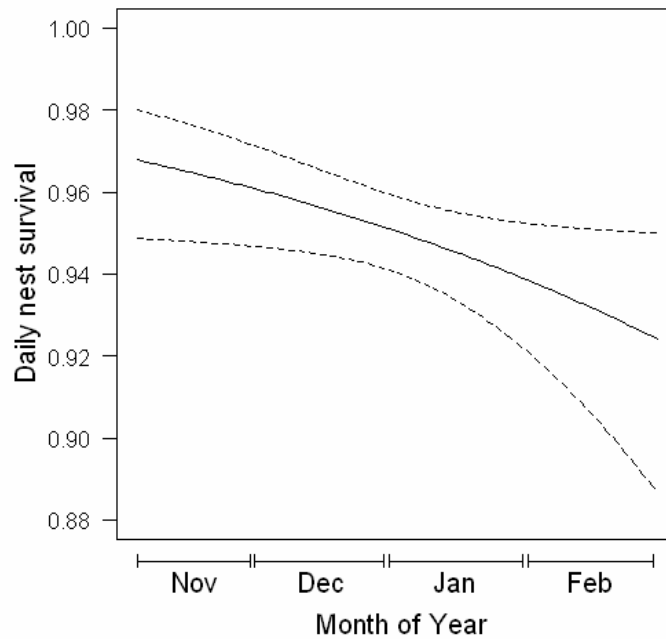
was some support for a quadratic relationship between nest survival and time during the season but the simpler model was favoured. This analysis is of two years' data covering the same period. There appears to be little variation between years (Model 17) so data have been pooled in other models. St. Helena Plovers were observed to re-nest on multiple occasions, both after failure and success of the previous breeding attempt. However the average number of nesting attempts pair<sup>-1</sup> year<sup>-1</sup> did not vary between sites (Kruskal-Wallis,  $\bar{x} = 1.97$ ,  $X^2_3 = 2.178$ ,  $P = 0.536$ ).

**Table 3** – *Nest survival model output from programme MARK*

<i>Model</i>	<i>Delta AICc</i>	<i>AICc Weights</i>	<i>Model Likelihood</i>	<i>Parameters</i>	<i>Deviance</i>
1: Site + day	0.0000	0.1897	1.00000	5	527.1871
2: Site + day <sup>2</sup>	0.2330	0.1688	0.8901	6	525.4079
3: Cat + day	0.3796	0.1569	0.8271	3	531.5850
4: Cat + day <sup>2</sup>	0.4739	0.1497	0.7890	4	529.6712
5: Site + day + age	1.5408	0.0878	0.4628	6	526.7157
6: Cat + day + age	1.7208	0.0802	0.4230	4	530.9180
7: Site + day <sup>2</sup> + age	1.8206	0.0763	0.4024	7	524.9813
8: Cat + age + day <sup>2</sup>	1.8876	0.0738	0.3891	5	529.0747
9: Site	6.5526	0.0072	0.0377	4	535.7498
10: Cat	7.6385	0.0042	0.0219	2	540.8499
11: Site + age	8.0970	0.0033	0.0175	5	535.2841
12: Cat + age	8.9916	0.0021	0.0112	3	540.1969
13: Day	17.1513	0.0000	0.0002	2	550.3628
14: Constant	19.5779	0.0000	0.0001	1	554.7934
15: Age	19.9830	0.0000	0.0001	2	553.1945
16: Nest camera	21.5565	0.0000	0.0000	2	554.7680
17: Year	21.5710	0.0000	0.0000	2	554.7825



**Figure 5** –The dotted line shows the relationship between nest survival and the index of cat density predicted using the cat only model (10 in Table 3). The points show the observed index of cat density for each site, and the nest survival for each site predicted from the site only model (9 in Table 3), arrows indicate 1 S.E.



**Figure 6** – Relationship between time in the season and nest survival predicted from MARK modelling; dotted lines show upper and lower 95 % confidence intervals.



## Discussion

Here we investigated the influence of introduced predators on the demography of an island endemic. Our study had three key findings. Firstly, several introduced species were recorded as nest predators, of these cats were the most important. Secondly, there was spatial variation in the densities of nest predators and variation in cat density was negatively correlated with nest survival. Thirdly, pairs at sites with low nesting survival did not respond to this by having a greater number of nesting attempts per year.

### *Nest predators*

We can make several general statements about the nest predators identified during this study. Firstly, all species recorded have been introduced to the island since 1502 (Ashmole and Ashmole 2000). That all nest predators are introduced is not unexpected as there are now no native species that are likely to be egg eaters, however, it does serve to show how much the fauna of St Helena has been altered since human colonisation. Secondly, all the species recorded are amongst those known to have had substantial negative impacts when they have been introduced elsewhere; all are included in a list of the top 100 invasive species (Lowe et al. 2004). Of the species recorded cats and rats are of particular notoriety. They have been linked to numerous past extinctions and declines (Courchamp and Chapuis 2003; Dowding and Murphy 2001; Towns et al. 2006), and are key threats to the fauna of the UK Overseas Territories (Hilton and Cuthbert 2010). The Common Myna has recently been recorded as the most frequent nest predator of Sooty Terns *Sterna fuscata* on St Helena's nearest neighbour, Ascension Island (Hughes et al. 2008). The swamping of St. Helena Plover nests by ants is an uncommon occurrence, having been observed on only four occasions out of 173 nests monitored. Nevertheless it is noteworthy, as although *Pheodole megacephala* has often been implicated in the decline of native ants and other invertebrates (Hoffmann et al. 1999; Hoffmann and Parr 2008; Wetterer 2007), evidence of direct impacts on vertebrates remains anecdotal (Plentovich et al. 2009; Wetterer 2007). Thirdly, two of the nest predator species are themselves linked by predation. Cats and rats are both predators of St. Helena Plovers but cats also prey upon rats. Thus it is likely that the numbers of both species are linked and the decline in the former, for example through control, could lead to an increase in the latter. This is an important consideration if any control were to be undertaken as a conservation management

technique; other studies have found a numerical response in mesopredator numbers following control on the apex predator (Courchamp et al. 1999a; Ritchie and Johnson 2009; Tompkins and Veltman 2006). An increase in rats could negate the benefit of cat reduction on nest survival; one study even recorded lower nesting survival in the presence of rats alone compared to both rats and cats (Rayner et al. 2007). Moreover, increasing the rat population is also likely to have negative impacts on species other than the St. Helena Plover, and a reduction in cats could also allow an increase in mice and rabbit populations. There are over 400 endemic invertebrates and around 50 endemic plant species on St Helena, some of which are currently threatened by rodents and rabbits (Ashmole and Ashmole 2000; Bell and Floyd 2009).

Finally, the main nest predator, cats, are generalist predators and on similar islands have been found to rely primarily upon other introduced mammals for food, in particular rabbits (Bergstrom et al. 2009; Molsher et al. 1999; Nogales and Medina 1996; Pontier et al. 2002). This has two implications, firstly, although cats may be eating a large proportion of the eggs of St. Helena Plovers the contribution of these eggs to the cat diet is likely to be small. Secondly, cat numbers are likely to track the availability of their mammalian prey (Harper 2004; Jones 1977) and be little affected by the size of the St. Helena Plover population. Large populations of rabbits and rodents may be allowing cat densities to reach heights that would not otherwise be sustainable, and therefore exert unprecedented predation pressure (Courchamp et al. 1999b; Oliver et al. 2009; Taylor 1979). Cat predation could be more severe per capita at smaller St. Helena Plover populations if cat density is independent of plover numbers. However, there is some evidence to suggest that nests will be found by cats at a rate directly proportional to nest density. Ground nesting bird nests have been found to be difficult for dogs and foxes to detect more than a few meters away (Seymour et al. 2003; Storaas et al. 1999) and fox and racoon predation on these nests has been proposed to be largely an incidental repercussion of foraging for other prey (Seymour et al. 2003; Vickery et al. 1992).

#### *Estimating Predator densities*

It is difficult to explain why the two indices of rat density showed significant correlation in pasture sites but not in the semi-desert. It has been suggested that wax blocks are most reliable when comparing across areas of similar habitat as biases are likely to be

minimized. Home range size in rats often varies between habitats, and Wilson (2007) suggested a negative relationship between population density and home range size and activity. A larger than average home range size and increased activity levels could allow a single rat to visit more than one station, thus biasing results. However, this does not explain the divergence of the two methods. It is possible that the dominant rat species varies between habitats. If this was true then the divergence could be explained by a differential response of each rat species to the survey methods, for instance due to different taste preferences; the chew sticks were soaked in vegetable oil and the wax blocks were impregnated with fish oil. The lower indices observed using chew sticks at the pasture sites may be partially explained by the observation that the bite marks on the chew sticks were less distinct than those on the wax blocks.

#### *Impact of nest predators on nest survival and productivity*

Nest survival was found to vary substantially and consistently across the island for the two years of the study, and relative cat density was found to predict site level nest survival. This relationship does not show causality and we must consider whether a third parameter, which co-varies with cat density, is more likely to cause the variation in nest survival. Nest survival does not differ consistently between the two habitat types, pasture and semi-desert (DWP, BB, MH versus UPB), which also tests between the presence or absence of livestock. There does not appear to be any strong correlations between nest survival and any climatic variable, for example elevation or rainfall. Our sample size is small, however, and within site variation in climatic variables is large and thus our ability to detect spatial patterns is limited.

Here we investigated whether St. Helena Plovers increased the number of re-nesting attempts in response to high nest predation, and found no effect. Birds can, however, also compensate for high levels of nest predation by having higher brood survival. Unfortunately, given the low nesting survival at some sites, an insufficient sample size of broods were followed to allow brood survival to be assessed at each site. However, no difference was found between the two habitats types (Burns 2011, Chapter 4). This largely amounts to testing for a difference between Prosperous Bay and Deadwood Plain, as the majority of broods were from these areas. In addition to the mechanisms discussed above, birds are frequently found to move location in response to nest predation (Lima 2009). This was not found to be the case in our study as St. Helena

Plovers are very site faithful once they have settled on a breeding territory. Breeding birds have only been observed moving to a new territory in a different site three times out of 104 adults ringed, 73 of which were re-sighted at least a year after ringing (Burns 2011, Chapter 4). Movement would only be adaptive if the current risk of predation predicts future risk, if there is spatial variation in predation risk, there are available territories in a lower risk area, and the birds can perceive this information. Although variation in risk exists, St. Helena Plovers are likely to be constrained from moving by the availability of suitable territories and therefore the cost of prospecting for another territory.

Roper et al. (2010) found that the highest selection pressure was predicted to be on reducing the re-nesting duration when nest predation was high and the breeding season long. A closely related species, the White Fronted Plover *Charadrius marginatus*, has been observed nesting up to 11 times in a year (in Lloyd 2008), so why do St. Helena Plovers not? Another environmental parameter may be limiting their ability to produce multiple clutches, and the most likely candidate is food availability. Food has regularly been seen to limit the total number of eggs that a female bird can lay in a single season (Newton 1998; Zanette et al. 2006b). Additionally, several studies have shown an interaction between food availability and predation risk. In high predator areas elevated food availability led to reduced nest predation (Zanette et al. 2006a) and faster chick growth (Dunn et al. 2010). It is thought that these interactions are driven by non-lethal effects of predator presence on prey behaviour. Although work has focussed on the trade-off between efficient foraging and mortality risk (Cresswell and Whitfield 2008; Dunn et al. 2010) a similar trade-off is seen between investment in reproduction and mortality risk (Scheuerlein et al. 2001; Sheriff et al. 2009; Travers et al. 2010). Therefore, St. Helena Plovers in areas of high predator density may be avoiding further nesting attempts to reduce their own risk of mortality. This theory is supported by the fact that adult survival was found to be lower at the site with the lowest nest survival, Man and Horse (Burns 2011, Chapter 4), indicating that the risk to incubating adults may be higher here. It is possible that high nest predation levels may simply have developed so recently that insufficient time has passed for the plovers to adapt to it. The plovers, however, exhibit adaptations associated with high nest predation, such as small clutch size. Furthermore, they are thought to descend from mainland African populations, where a wide range of predators would have been present. Additionally, it

is thought that at least one of the endemic rail species on St Helena could have been an egg predator (Olson 1975). If birds in areas of high nest predation are on average of poorer quality then this could also explain the absence of an increase in the number of nesting attempts pair<sup>-1</sup>. For instance, it is quite common for productivity to increase with age in birds (de Forest and Gaston 1996; Weimerskirch 1990). A higher level of between site movements of adult birds than that observed would be required, however, in order to maintain differences in the average age of birds between sites.

If brood survival does not exhibit considerable variation between sites then annual productivity will be directly proportional to nest survival. St. Helena Plovers have relatively low annual adult mortality, average 0.171 (Burns 2011, Chapter 5). If we assume constant brood survival between sites (0.348 - Burns 2011, Chapter 6), a rough estimate of annual productivity can be estimated using the nest survival and breeding attempts per year presented in this paper. These estimates vary among sites between 0.0425 and 0.213 fledglings pair<sup>-1</sup> year<sup>-1</sup>, therefore populations at some sites are not producing sufficient fledglings to counterbalance adult mortality, even prior to mortality in the first year post-fledging being taken into consideration. Therefore, we can see that populations at different sites vary in their ability to offset adult mortality through production and that production varies between sites largely due to differences in nest survival, which is itself correlated with cat density. From this we can infer that cat density is playing a part in limiting the population of St. Helena Plovers, at least locally. The population at each site could remain stable under these conditions if dispersal between areas was common. Although the movement of adults is rare, post-natal dispersal is common and juvenile birds have been observed moving between all areas of the island (FB, unpublished data). This implies that the whole island is acting as a single metapopulation with a matrix of sink and source populations (Hanski 1998; Pulliam 1988). Whether the movement of young birds to sink areas is having a limiting effect on the whole metapopulation remains unknown at present and will depend on the balance between productivity and mortality in each site and the dispersal rules used by juveniles. Investigating these possibilities will be the subject of future work.

### *Conclusions*

Our data indicate that the negative impact of introduced species on oceanic islands is continuing. The annual productivity of St. Helena Plovers varies between different

areas of the island, and in some areas productivity was limited to below that which would balance out adult mortality, leading to sink and source dynamics. This limitation in productivity appears to be largely controlled by variation in nest predation, which is linked to the relative abundance of the most important nest predator, cats. Plover productivity may also be influenced by food availability or the non-lethal impacts of predator presence.

This suggests two possible routes to increased productivity in sink areas: reducing predator densities or increasing food availability. Reducing predator densities could be problematic since the nest predator community contains both apex (cat) and mesopredator (rat) species and therefore it is difficult to predict the ecosystem level implications of control. Increasing food availability would therefore appear a more attractive option. However, it is not clear how this could be achieved without markedly altering the habitat. Increasing stocking densities, in particular of cattle, may lead to an increase in the St. Helena Plover's invertebrate prey and may also reduce rodent density; however, stocking densities must remain relatively low on St Helena in order to prevent excessive soil erosion or elevated nest trampling rates (Beintema and Muskens 1987). An intriguing option is to undertake both conservation options simultaneously, as doing so has shown synergistic effects on productivity (Newton 1998; Zanette et al. 2006a). A final option, not investigated here, would be to attempt to manage the habitat (here meaning the floral distribution and structure), either to discourage high densities of predator species, or to increase the total amount of habitat available in the source areas.

Our study suggests two avenues for future work, firstly to understand the implications of reducing the number of feral cats, either through population modelling or small scale experimental trials. Secondly, investigate how other aspects on the environment influence productivity, for example food availability or vegetation structure, as altering such parameters could lead to a much more sustainable and less controversial solution to low productivity.

## Acknowledgements

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### **Chapter 3: Influence of habitat on nest survival and distribution of the St. Helena Plover *Charadrius sanctaehelenae***

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TS: Manuscript improvement

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NM: Data collection, manuscript improvement

## **Abstract**

Understanding species habitat requirements and how habitat change has affected, or may affect species persistence, is critical to the preservation of global biodiversity. Here we investigate how habitat characteristics shape the current spatial distribution of the breeding habitat of the endangered St. Helena Plover, and ask how previous habitat change has affected habitat suitability for this species. A habitat suitability model was developed using programme MaxEnt. The model was parameterised using point data values for vegetation cover and topography. The resulting MaxEnt model was informative, with average test AUC of 75 %. Vegetation height was the most important vegetation parameter in the MaxEnt model, with habitat suitability declining rapidly with increasing height. It is thought that the plovers are selecting short vegetation both to maximise visibility around the nest and to increase the availability of their invertebrate food. Elevation and slope were also important determinants of suitable habitat. Elevation is not influencing suitability directly and it is likely that it correlates with variation in predator densities and rainfall. Change in habitat suitability partially explained the change in bird density over time, indicating that habitat deterioration may in part account for the recent decline in population numbers. Nevertheless, it is likely that other factors were also involved. Habitat was seen to primarily influence the distribution of territories rather than productivity; no habitat parameters explained variation in nest survival over the ranges observed. Furthermore, the current total area of suitable habitat was estimated to be significantly larger than that required to support the present population, indicating that habitat availability is not currently limiting the population.

## Introduction

Anthropogenic habitat change is cited as the most important current threat facing biodiversity (Pimm and Raven 2000), and has been a major contributor to historic vertebrate extinctions. For example 19 out of 80 bird extinctions of attributable cause since 1600 have been linked to habitat change (Johnson and Stattersfield 1990). Habitat change can be particularly pronounced on isolated island ecosystems following their discovery by humans. In order to conserve the species that remain it is essential that we understand how anthropogenic habitat change has altered the suitability of the environment for different species and therefore how the habitat should be managed to maximise suitability in the future. One way to address these questions is to develop a habitat suitability model.

Habitat suitability models have been used for a variety of purposes, including: to predict the current distribution of suitable habitat for the purposes of risk assessment or to estimate population size or threat status (Gavashelishvili and Javakhishvili 2010; Long et al. 2008; Pearce-Higgins et al. 2009); to understand environmental associations (LeDee et al. 2008; Milsom et al. 2000); or to forecast predicted changes in distribution under novel environmental conditions (Yates et al. 2010). There are two general computational methods for habitat suitability models, and these are usually linked to the type of data used. Traditional statistical approaches, such as logistic generalised linear or additive modelling require information about both the characteristics of areas where the species is present and areas where it is absent. Alternatively, Machine Learning approaches, such as GARP (Genetic Algorithm for Ruleset Prediction, Stockwell and Peters 1999), ENFA (Ecological Niche Factor Analysis, Hirzel et al. 2002) or MaxEnt (Maximum Entropy, Phillips et al. 2006), use only presence data, often accompanied by information describing the wider landscape, termed background data. Machine Learning is a group of methods that allow a computer to generate rules, or generalisations from the empirical data supplied. In this case the empirical data are the values for the environmental covariates for the presence samples and those for the landscape as whole (background samples). This is in contrast to traditional statistical methods where the functional relationships thought to be present in the data are described a priori. Machine Learning techniques are particularly useful when there are many potential explanatory variables, or when the functional relationships are difficult



to assess a priori or are complex. There is currently considerable debate about whether absence data should be used in species distributions models (Boyce et al. 2002; Elith et al. 2011; Zaniwski et al. 2002). Nevertheless, in general the use of presence and background data, rather than presence and absence data, is supported when the objective of the study is to map the potential distribution of a species, rather than the current distribution. The potential distribution is greater than the current distribution as it includes areas of potentially suitable habitat, based on the recorded values of the environmental parameters, but that are currently unoccupied.

This paper describes a habitat suitability model for the St. Helena Plover *Charadrius sanctaehelenae*, an island endemic restricted the Atlantic island of St Helena (15 58'S 5 43'W). Since the discovery of St Helena by humans in 1502 the island has undergone dramatic changes, and current habitats are largely anthropogenic (Cronk 1989). The primary agent of habitat change on St Helena has been deforestation, for conversion to agricultural land, for fuel and through browsing by introduced herbivores. Deforestation has led to large areas of badly eroded semi-desert. These areas, locally termed the Crown Wastes, make up 70 % of the present day land cover (McCulloch 1992). This habitat change has, in part, led to the extinction of all St Helena's endemic bird species that were present in 1502 bar the St. Helena Plover (Olson 1975). The St. Helena Plover is currently classified as Critically Endangered due to a rapid decline in numbers between 2000 and 2005 (BirdLife International 2009; McCulloch 2009). More recent censuses indicate that the species is no longer declining but remains vulnerable (SHNT 2011). The St. Helena Plover is a bird of largely open habitats and as such is likely to have benefited from historic deforestation on St Helena (McCulloch 1992). However, in addition to historic habitat change there has also been recent change, in particular on pasture areas. Agricultural production in general has declined, as have stocking densities, which has led to scrub encroachment and an increase in overall vegetation height (McCulloch and Norris 2002). These changes may partly explain the recent decline in population numbers. Previous studies, however, did not observe concurrent change in important habitat parameters and bird density (McCulloch and Norris 2001).

Using new data we created a habitat suitability model for this species using MaxEnt. We used this model for three purposes: to gain a better understanding of how habitat

characteristics influence bird distributions, to assess the current area and spatial distribution of suitable habitat and to predict how suitability has changed over time. Because the current population size of St. Helena Plovers is low, there are likely to be currently unoccupied areas that contain suitable habitat, therefore our aim in this study was to map the potential distribution of suitable habitat. We thus chose to use a presence and background method. We chose to use Maxent because it has consistently been found to perform well compared to other methods (Elith 2006).

As well as influencing species distributions, environmental variables can influence species demography. Therefore we investigated whether variation in nest survival could be explained by habitat suitability in the vicinity of the nest.

In summary, our study investigated the following questions:

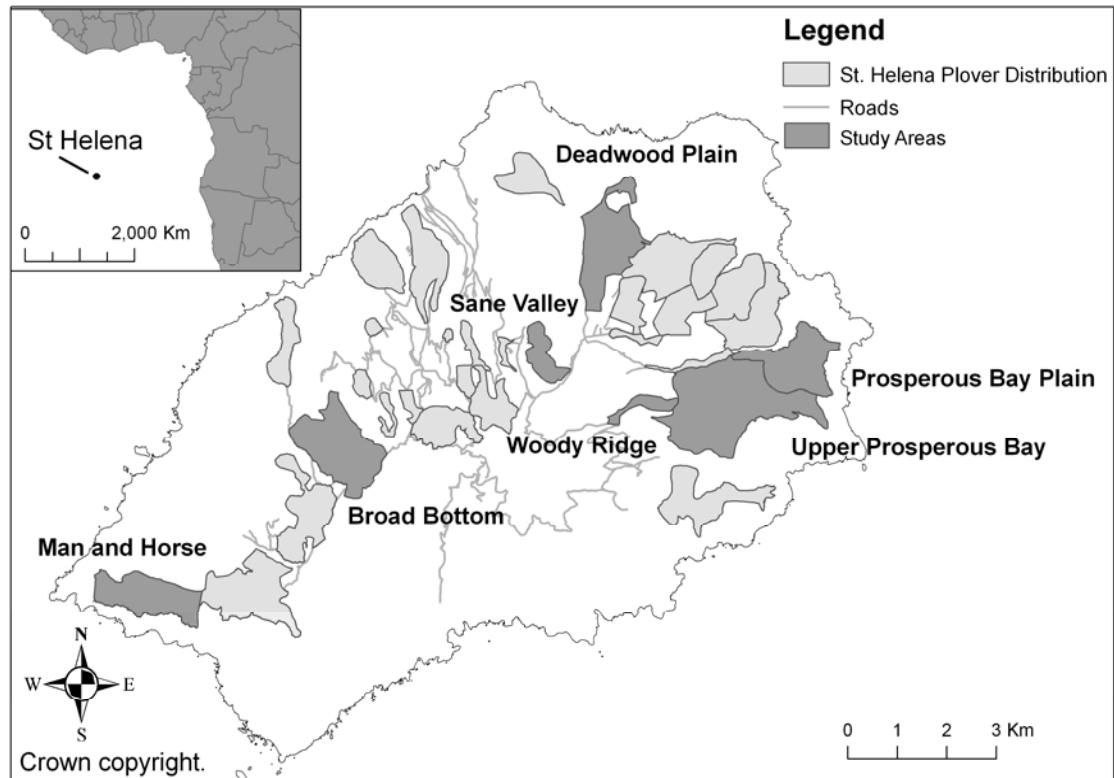
1. What are the key determinates of habitat suitability for the St. Helena Plover?
2. What is the current area of suitable nesting habitat for St. Helena Plovers within our study areas?
3. Does variation in habitat influence the productivity of St. Helena Plovers?
4. To what degree can change in the density of birds be explained by concomitant change in vegetation composition and structure?

## **Methods**

### *Data collection*

Habitat surveys used to construct the habitat suitability model were undertaken during November 2008. They were conducted at several sites of each of the two main habitat types, semi-desert (Prosperous Bay Plain, Upper Prosperous Bay) and pasture (Deadwood Plain, Broad Bottom, Man and Horse, Sane Valley and Woody Ridge, Figure 1). Vegetation composition was recorded at randomly located quadrats, 0.25 m<sup>2</sup>, at a density of one hectare<sup>-1</sup>; sample size is shown in Table 1. The location of the first quadrat at a site was randomly selected. A series of distances (1-100 paces) and directions (clock-face 1-12) were randomly generated and used to determine the location of subsequent quadrats. At each site a prominent distant landmark was used as a reference point for the clock-face, marking 12 o'clock. At large sites the location of the first quadrat of each group of ten was subjectively selected to ensure an even

distribution. Vegetation height was measured every 0.5 m in a 10 m transect randomly orientated from every fifth quadrat, with bare ground taken as a height of zero. An estimate of vegetation height was obtained for each quadrat location by interpolating the height data to a coverage using inverse distance weighting (IDW); cell size 35 m. Interpolation creates a grid of squares (dimensions specified by the cell size) across the entire survey area, and it uses the point estimates at each quadrat to calculate the associated value for each cell of the grid. The inverse distance weighted method calculates each cell's value using a weighted average of those point estimates surrounding the cell, with point estimates further from the cell contributing less weight to the calculation than those close by. Survey methods followed those used by McCulloch (2009) and McCulloch and Norris (2001) to allow comparison. For a sample of plover breeding territories nine quadrats (5 m apart) were recorded around the nest in a 3x3 grid, recording equivalent information as for the site as a whole. These territory level data were used in the analysis of nest survival only. At each quadrat the GPS location was recorded and percentage cover of each vegetation type noted. Vegetation categories were: bare ground, rock, gravel, grass, broadleaved herbs, dwarf shrub (up to 50 cm), and shrub (shrubs or trees taller than 50 cm). *Carpobrotus edulis*, locally known as creeper, is a mat forming succulent that is spreading rapidly across the semi-desert and therefore was identified separately in two categories, live and dead. The dead material makes up around half of the area covered by creeper and it becomes very dry and breaks down slowly (McCulloch 1991).



**Figure 1** – Map showing the known distribution of the *St. Helena Plover*, with the location of study sites in darker grey and the location of *St. Helena* inset.

McCulloch and Norris (2001) suggested that habitat change had been measured at too large a scale previously, therefore we compared habitat and bird density at the level of field at the most important pasture site, Deadwood Plain; previous studies have averaged habitat composition by study site. For this analysis the above data were supplemented by corresponding information collected between December 1998 and December 2000 (hereafter referred to as 1999) and during December 2005; methods described in McCulloch and McCulloch and Norris (2009; 2001). During these previous studies vegetation had been identified to species and was therefore grouped into the categories described above to allow comparison. Each time Deadwood Plain was visited during routine work a count of birds was recorded at the level of field, although not all of the 19 fields were covered on each visit. An average of these field-level counts was taken for each of the two of the three time periods investigated, 1999 and 2008. During 2005 the study period was limited and a single census of all of Deadwood Plain was used. These counts were expressed as densities by dividing them by the area

of each field. Both counts and habitat variables were collected during the summer months on St Helena which form the core breeding season of the plovers.

Nest survival was monitored at three pasture sites: Deadwood Plain, Broad Bottom and Man and Horse, and two semi-desert sites: Upper Prosperous Bay and Prosperous Bay Plain. The two semi-desert areas are contiguous and were pooled into a single site named Prosperous Bay during nest survival analysis. Nest survival was monitored throughout the core breeding season for St. Helena Plovers, November to February. Nest survival data were collected for two years, starting in November 2007 and 2008. Methods follow that of Szekely (2007b) and are described more fully in Burns (2011, Chapter 2, 4).

#### *Habitat suitability model*

Each quadrat in the 2008 survey was allocated as either within a current plover territory or not. Quadrats within 75 m of a known plover breeding attempts were classified as presences (Table 1); all quadrats were included as background data. Estimates of slope and elevation for each quadrat location were extracted from a triangulated irregular network based on a 10 m contour map of St Helena. The basic procedure used by MaxEnt is as follows. During each iteration of the MaxEnt model a probability distribution, based on the full set of environmental input parameters, is created, mimicking the empirical distribution of the input data. There will exist many ways to approximate the empirical distribution, for instance using different combinations of functional relationships (linear, or quadratic), or using different sets of interactions between the input parameters. Therefore, the distribution resulting from each model iteration will be different. From this set of output distributions the one which most closely represents the empirical distribution of the background data is selected. In this way MaxEnt is trying to minimise the difference between the probability distributions of the presence data and that of the overall landscape, subject to the constraints of the presence data (Elith et al. 2011). In other words MaxEnt is seeking the simplest model that still adequately explains the observed presence data, and therefore it is similar to the theory of parsimony in traditional statistics. The resulting MaxEnt model generates a Habitat Suitability Index (HSI: 0-1) for each presence and background location, giving the relative suitability of each location.

Although other options were investigated, default settings for regularisation and functional types were used in MaxEnt. Modelling was conducted for pasture sites and semi-desert sites together. The model was constructed using ten fold cross-validation. During each replicate 70 % of the presence data were randomly selected as the training set; and the remainder were used for model testing. Model robustness was tested by creating a ROC curve (Receiver operating characteristic), and calculating the AUC (area under the ROC curve). The AUC is an indication of how good the model is. An AUC of 50 % means the model is no better at predicting the species distribution than random; values higher than this indicate increasing predictive ability. Since we are predicting potential distribution from presence data only, the maximum possible AUC is less than 1 (Wiley et al. 2003). The influence of each explanatory variable on habitat suitability is assessed in MaxEnt using two metrics, percent contribution and permutation importance. The percent contribution is the increase in gain from the addition of a model parameter summed over all model iterations. Gain is a measure of the goodness of fit of the model, with higher values indicating a better fit. Permutation importance is calculated as the percent that the AUC is reduced by if the values of the parameter in the presence and background data are randomly permuted.

From the model output we obtained an estimate of the habitat suitability index (HSI) for each quadrat location at which vegetation was measured in 2008. For presence only models the HSI indicates relative suitability rather than the probability of that habitat patch being occupied. This is because it is not possible to estimate overall prevalence in the study area using a presence only method. Using inverse distance weighting we interpolated these point data to cover all areas of the study sites, cell size 10 m. The output of MaxEnt is on a continuous scale of 0-1 and various rules have been developed to calculate threshold values to convert this continuous scale to a binary distinction between suitable and unsuitable habitat. The threshold method used can substantially alter the conclusions taken from the model and therefore we considered two methods from a group of those found to have superior performance (Liu et al. 2005). Here we considered the equal sensitivity and specificity and the maximum sum of sensitivity and specificity methods, for both the training and testing datasets. Using this threshold and the interpolated raster layer of HSI, the area of suitable habitat was estimated for each site. We also used the resulting habitat suitability map to visually assess whether there

were substantial areas of any site that contained suitable habitat but nevertheless were not currently being used by the plovers.

**Table 1** – *Total number of quadrats undertaken at each study site and the number classified as presence samples*

<i>Site</i>	<i>Quadrats</i>	
	Total	Presence
Deadwood Plain	210	95
Broad Bottom	220	39
Man and Horse	140	45
Sane Valley	40	0
Woody Ridge	20	3
Prosperous Bay Plain	155	12
Upper Prosperous Bay	360	107
<b>Total</b>	<b>1145</b>	<b>301</b>

#### *Change over time at Deadwood Plain*

All statistical analysis was conducted in Programme R unless otherwise specified (R Core Development Team 2004). Vegetation data were summarized by calculating the mean value for each field for each of the three time periods. The mean was chosen over the median as the latter led to an overabundance of zero values for many of the variables. We constructed a linear mixed model with bird density as the response variable. The percent composition of the main vegetation categories (grass, broadleaved herbs, dwarf shrub, shrub and un-vegetated), vegetation height and the first order interactions between these variables were explanatory covariates, and year an explanatory factor. Field was incorporated as a random term to account for pseudoreplication. The full model was simplified using backwards selection. The parameter whose removal would result in the greatest drop in AIC was chosen for deletion each time. ANOVA tests were used to ensure that each model simplification was justified.

Using the results of this initial regression model to isolate the most important parameters, the change in these parameters and in bird density were calculated between time period 1-2 and period 2-3 for each field. A linear mixed model was used to

investigate if change in the important habitat variables explained a significant amount of variation in concurrent change in bird density. This change analysis also included an explanatory factor of time period, first order interactions between time period and vegetation categories, and a random term of field. Simplification of the full model was conducted using the same procedure as described above. The MaxEnt model was used to predict the HSI for each field at Deadwood Plain for each of the three time periods. The change over time analysis was then repeated using change in HSI as an explanatory variable and time period as a factor.

#### *Nest survival analysis*

In order to investigate if the vegetation composition in the vicinity of a nesting attempt influences the nest's fate, an analysis of nest survival was conducted, using those habitat variables that had been shown to be important during previous analyses. The HSI was also included as an explanatory variable in order to test whether nest survival was higher where the habitat was more suitable, as estimated from the occupancy data. In order to obtain an estimate of each explanatory variable at the location of each nest, inverse distance weighted layers were constructed for the key vegetation parameters by interpolating the 2008 quadrat data (cell size 35 m), including data measured at specific territories. Using these layers and that constructed previously for the HSI, the habitat characteristics associated with the location of each breeding attempt were extracted. Analysis of nest survival was carried out using programme MARK (White and Burnham 1999). Since HSI cannot be considered in the same model as the individual vegetation parameters two full models were considered. Both models contained site identity and year as explanatory factors, in addition the first contained the vegetation covariates and the second contained the HSI. The full models were simplified using the backward selection process described previously.

## **Results**

#### *Habitat suitability model*

Table 2 summarises the input presence and background data to the MaxEnt model and Table 3 shows the results of the MaxEnt model, indicating the relative importance of each explanatory variable in determining habitat suitability. The average test AUC (74.6 %, SD = 2.52) from the ten rounds of cross-validation was significantly above 50



% and therefore the model describes the species distribution substantially better than by chance alone. The percent contribution and permutation importance in general show agreement as to which input parameters are of importance. Elevation is the most important parameter in the final model, with suitability initially rising sharply with increasing elevation before levelling out between 400 - 600 m and then declining again (Table 3, Figure 2). Mean vegetation height is the most important vegetation variable, with a sharp decline in suitability for heights greater than 7cm. Percent shrub cover is also important as is degree slope; both exhibit an inverse relationship with suitability that is approximately linear. The coverage of grass also appears to have some explanatory value. Here there is an overall increase in suitability with increasing grass cover, however at values above 90 % the suitability drops off. The remaining explanatory variables are of little importance.

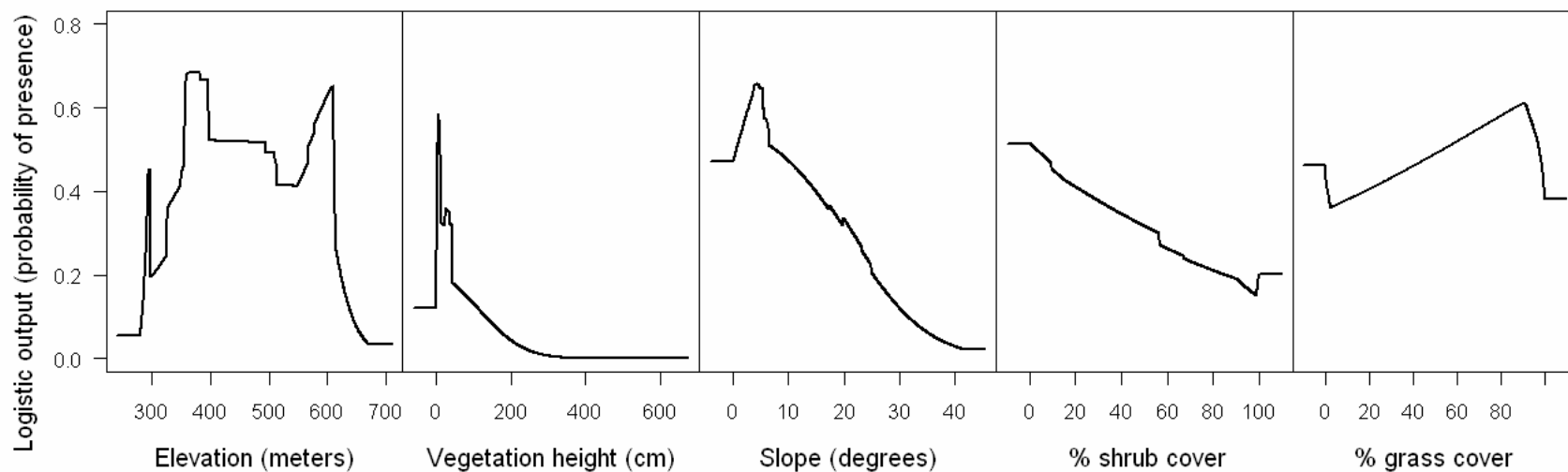
Figure 3 shows the IDW coverage of the distribution of the habitat suitability index across the study sites. From this figure it is clear there is a great deal of heterogeneity both between sites, and within each site, in how suitable the habitat is for the plovers. The four estimates of the threshold between suitable and unsuitable habitat considered were similar (range 0.401 - 0.461), and thus we took an average of these as the threshold value; 0.424. Therefore the two darkest shades of grey in Fig. 3 can be considered suitable and the lighter shades unsuitable. Using this threshold the proportion of each site that is currently suitable was estimated (Figure 4), and the total area of suitable habitat in our study sites calculated; 275.04 hectares.

**Table 2** – Mean values for each habitat parameter

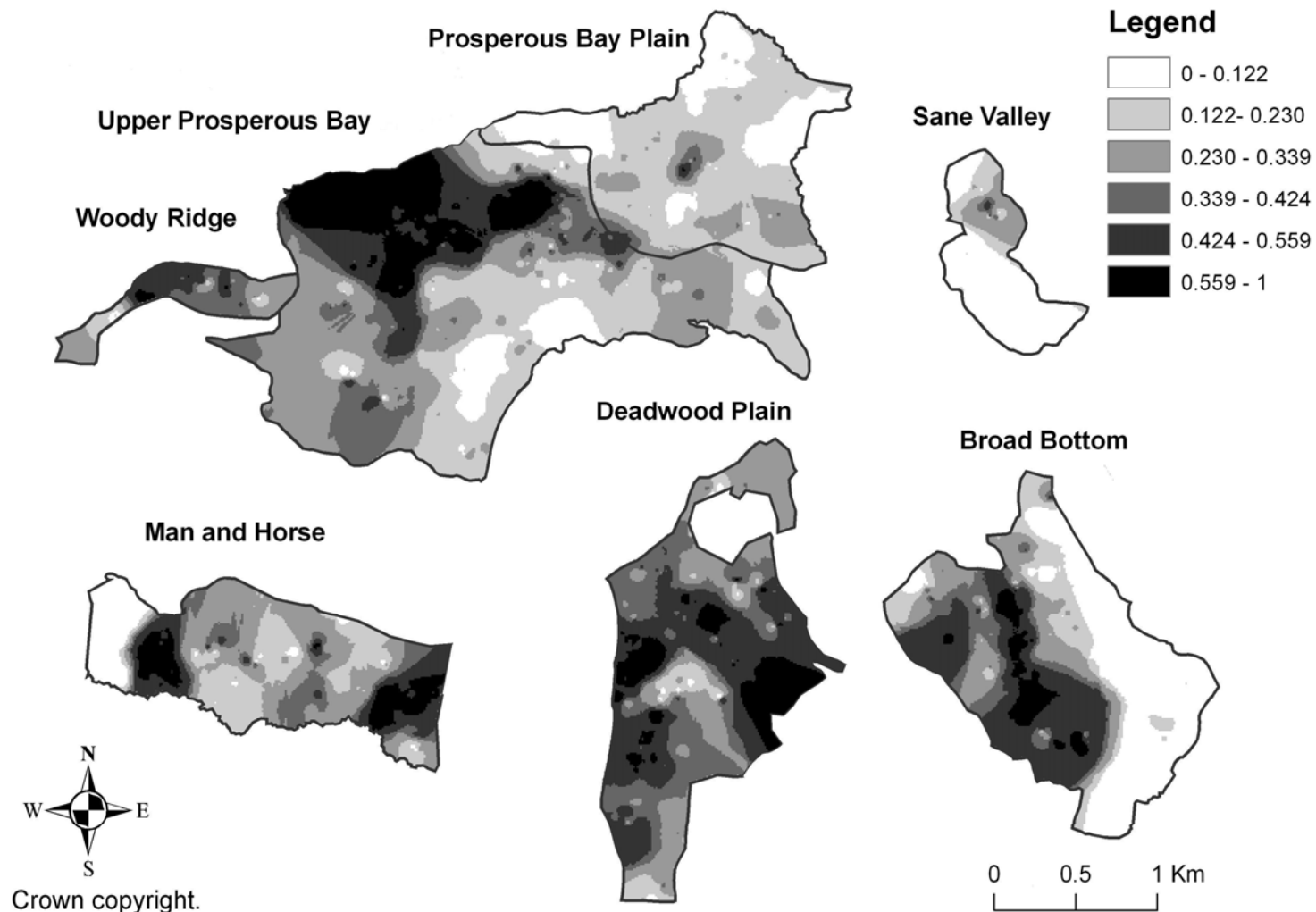
<i>Variable</i>	<i>Semi-desert</i>		<i>Pasture</i>	
	Presence	Background	Presence	Background
Elevation (m)	348.754	329.965	506.489	513.692
Mean vegetation height (cm)	4.902	4.0107	10.513	28.866
Slope (degrees)	5.096	6.536	9.0466	12.448
% shrub	5.269	4.565	1.742	11.591
% grass	0.126	0.971	75.769	69.638
% creeper	17.395	13.107	2.6978	2.425
% creeper (dead)	5.849	4.678	0.2473	0.187
% broadleaved herbs	0.0168	0.107	6.1429	4.533
% bare ground	35.773	39.489	10.725	9.289
% gravel	8.353	11.528	0	0
% rock	6.513	11.202	1.2198	0.895
% dwarf shrub	19.252	12.854	0.418	0.216

**Table 3** – Output of the final MaxEnt habitat suitability model.

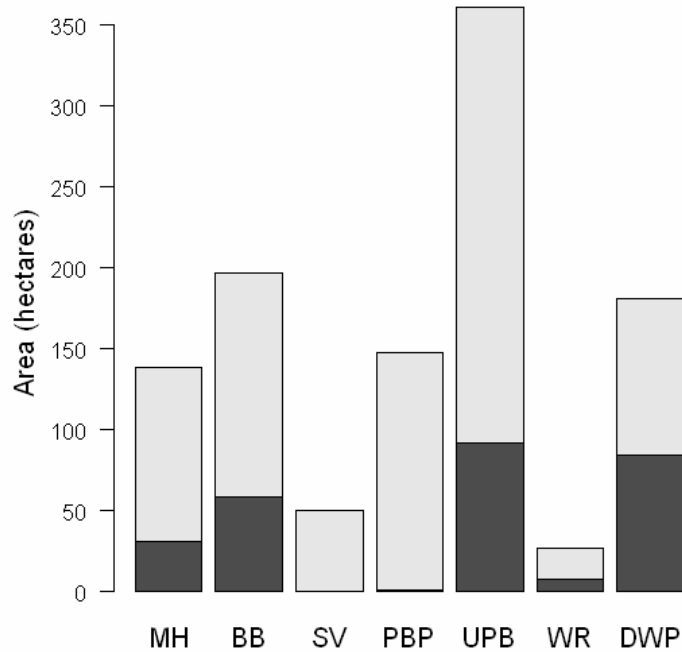
<i>Variable</i>	<i>Percent contribution</i>	<i>Permutation importance</i>
Elevation	37.3	26.6
Mean vegetation height (cm)	25.9	11.9
Slope (degrees)	19.9	14.9
% shrub	4.9	9.4
% grass	2.9	8.4
% creeper	2.1	6.3
% creeper (dead)	1.8	5.6
% broadleaved herbs	1.6	5.4
% bare ground	1.1	1.4
% gravel	1.1	7.3
% rock	1	1.4
% dwarf shrub	0.5	1.3
Habitat (factor)	0	0



**Figure 2** – MaxEnt model output showing the habitat associations for the five most influential parameters in the model. The plots are derived from model runs using each parameter in isolation. MaxEnt treats values outside the training range as if they were at the limit of the training range; this is termed clamping and is shown in the figures by horizontal lines extending from either end of each distribution.



**Figure 3** – Map showing the distribution of the Habitat Suitability Index derived by interpolation from the results of the MaxEnt model. Higher values and darker shades indicate more suitable habitat.



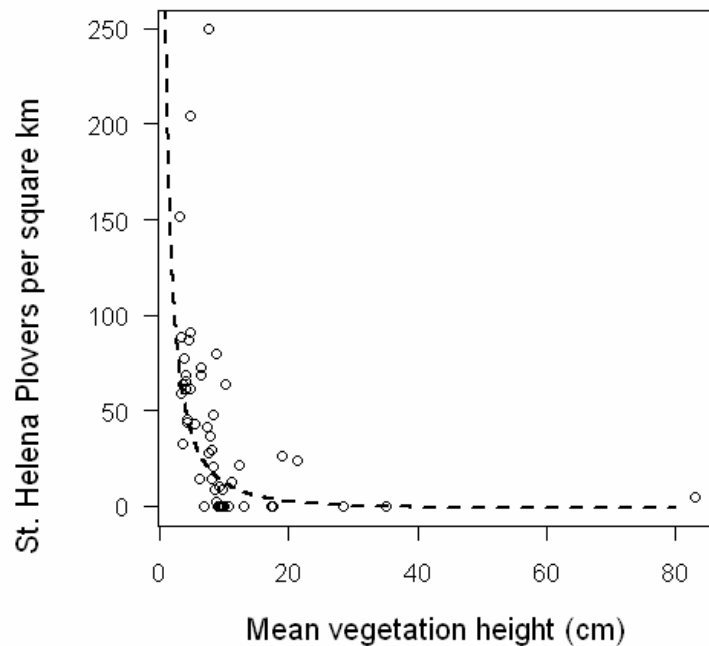
**Figure 4** – *Proportion of each site that is currently in suitable (dark grey) and unsuitable (light grey) condition. Sites are named: MH – Man and Horse, BB – Broad Bottom, SV – Sane Valley, PBP – Prosperous Bay Plain, UPB – Upper Prosperous Bay, WR – Woody Ridge and DWP – Deadwood Plain,*

#### *Change over time*

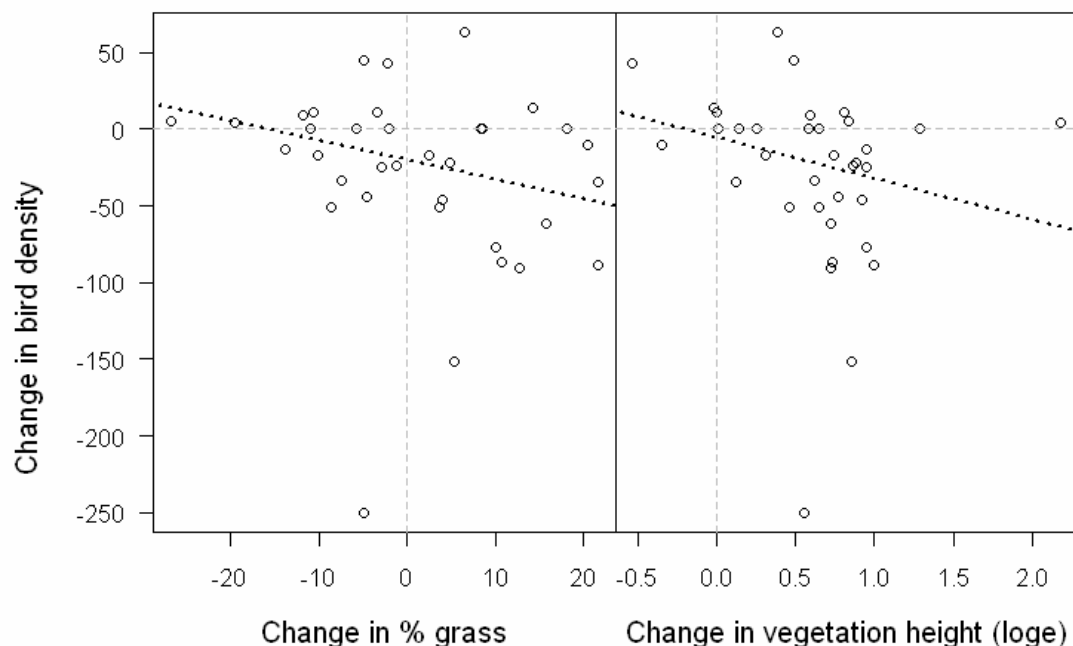
Vegetation height was the strongest predictor of plover density (Table 4, Figure 5), showing a rapid decline in bird density as mean vegetation height increased. Both percent shrub cover and percent grass cover also showed negative relationships with bird density over the range of values measured.

**Table 4** – Linear mixed model of *St. Helena Plover* density Random effects – field. The minimum adequate model is presented.

Response: Birds per km <sup>2</sup> – transformed			Observations: 54, fields: 19		
Fixed Effects	Estimate	S.E	DF	t-value	P
Intercept	6.055281	0.6664307	32	9.086137	<0.001***
Mean vegetation height (log <sub>e</sub> )	-0.572569	0.0959335	32	-5.968396	<0.001***
% grass	-0.020885	0.0059397	32	-3.516233	0.0013**
% shrub(log <sub>e</sub> )	-0.186875	0.0660641	32	-2.828689	0.0080***



**Figure 5** – Relationship between bird density (birds per km<sup>2</sup>) and mean vegetation height



**Figure 6** – *Change in % grass cover and mean vegetation height from one time period to the next linked to the change in St. Helena Plover density (birds per km<sup>2</sup>) over the same time period.*

Figure 6 illustrates the change in vegetation height and percent grass cover associated with changes in bird density at Deadwood Plain. There is one conspicuous outlier in both figures; this is from a very small field that had several birds present in 2005 but none in 2008. Change in vegetation height, grass cover and shrub cover all explained a significant proportion of variation in change in bird density when this outlier was removed (Table 5). When the change in HSI was investigated, outliers were also present, again for a small field. When the records for this field were removed there was a significant positive relationship between change in HSI and change in bird density. These relationships appeared to be sustained over time as time period and its interactions were not retained in either of the minimum adequate models.

**Table 5** – *Linear mixed model of change in bird density over time, first for vegetation parameters and then for HSI, Random effect – field in both cases. The minimum adequate model is presented in each case.*

<i>Response: Change in birds per km<sup>2</sup> - transformed</i>					Observations: 34, fields: 19
Fixed effects	Estimate	S.E	DF	t-value	p-value
Intercept	0.0860733	0.14704	18	0.5858	0.5656
Change in % grass cover	-0.03152	0.007720	12	-4.08267	0.0015**
Change in mean vegetation height (log <sub>e</sub> )	-0.5973	0.1949	12	-3.06476	0.0098**
Change in % shrub cover (log <sub>e</sub> )	-0.2995	0.07488	12	-3.9991	0.0018**

<i>Response: Change in birds per km<sup>2</sup> - transformed</i>					Observations: 33, fields: 18
Fixed effects	Estimate	S.E	DF	t-value	p-value
Intercept	-0.1840	0.1336	17	-1.3768	0.1864
Change in habitat suitability index	2.0645	0.7362	14	2.8041	0.0141*

Figure 7 shows the HSI by field in Deadwood Plain for each of the three time periods. The two lightest shades of grey are unsuitable habitat and the others are suitable. Fig. 7 shows a marked overall decline in suitability between 1999 and 2005; however the change is less clear change between 2005 and 2008, with some fields increasing in suitability and some declining.





**Figure 7** – *Habitat suitability over time at Deadwood Plain. The darker the shade of grey the more suitable the habitat in that field is. Two fields were not surveyed in 1999 and so are left blank.*

**Table 6** – *MARK output for pasture nests showing the results of all models considered*

<i>Model</i>	<i>Delta AICc</i>	<i>AICc Weight</i>	<i>Model Likelihood</i>	<i># Par</i>	<i>Deviance</i>
1: Site	0.00	0.350	1.000	4	498.080
2: Site + % grass cover	1.22	0.190	0.544	5	497.288
3: Site + habitat suitability index	1.47	0.168	0.481	5	497.534
4: Site + % grass + % shrub	2.22	0.116	0.330	6	496.274
5: Site + year + habitat suitability index <sup>1</sup>	2.74	0.0890	0.254	6	496.795
6: Site + year + % grass + & shrub	3.44	0.0627	0.179	7	495.483
7: Site + year + % grass + height + % shrub <sup>1</sup>	5.43	0.0232	0.0662	8	495.453
8: Constant	12.04	0.00085	0.0024	1	516.141

1: Full models

#### *Demographic analysis*

None of the vegetation parameters were significant predictors of nest survival in the MARK analysis (Table 6), nor was the HSI. The best model included only site identity. It is common practice to consider that the variables contained in all models within 2 AIC units of the minimum are informative (Burnham and Anderson 2002). Two

additional models in Table 6 meet this criterion; model 2 and model 3. However confidence intervals around the coefficient estimates for percent grass cover and HSI in these models span zero, and therefore little importance can be given to these variables. Additionally, the addition of these extra parameters results in a very small drop in model deviance suggesting that little additional variation in nest survival is explained.

## Discussion

This study produced three important results. First, we showed that the most suitable habitat for the St. Helena Plover has short vegetation, shallow slope and low shrub cover. This result is not entirely surprising, given that most *Charadrius* species breed in short grassy or barely vegetated sites (e.g. Prindiville Gaines and Ryan 1988; Tulp 1998). Second, we also showed that habitat suitability substantially changed since 1999, and these changes coincided with changes in bird density, suggesting that habitat change was in part responsible for the recent population decline in this species. Third, habitat suitability around the nest did not predict nest survival, although the range of input values over which this was estimated was restricted.

Habitat selection is likely to be partly determined by the habitats present during a species' evolutionary past. However, the natural habitats of St Helena are not well known and it is not known when the ancestral birds colonised the island. The St. Helena Plover is considered to form a super-species with the Kittlitz's Plover *C. pecuarius* and the Madagascar Plover *C. thoracicus* (McCulloch and Norris 2001) and therefore current habitats used by these species may give some indication of past habitat use by St. Helena Plovers. African *Charadrius* species are much less well studied than European or North American species. Nevertheless, it is known that present day populations of Kittlitz's and Madagascar Plover nest in dune habitats (Kittlitz's, Tulp 1998), and on open grasslands and dry mud flats around mangroves and alkaline lakes (Madagascar, Zefania et al. 2008). It is therefore likely that nesting on managed grassland is a recent transition for the St. Helena Plovers. However, prior to habitat change in the past few decades, the grazing pasture on St Helena that supports the greatest number of plovers was sparsely vegetated and therefore may not have been very different to dune or dry grassland habitats.

### *Habitat suitability model*

Our habitat suitability model is the first time that topography has been investigated alongside vegetation composition and structure for the St. Helena Plover. The high AUC values obtained indicate that the model can predict currently suitable habitats in the landscape with reasonable accuracy.

The choice of a breeding territory is likely to be a balance between resource availability, primarily food, and vulnerability to predation; the requirements of both are likely to vary between life stages. St. Helena Plovers have previously been seen to avoid setting up territories in areas of tall vegetation (McCulloch 2009; McCulloch and Norris 2001), and studies of other wader species on grassland have also found a strong negative relationship between presence and vegetation height (Beauvais and Smith 2003; Galbraith 1988; Milsom et al. 2000). In particular, waders during the non-breeding season have been seen to choose short swards (Colwell and Dodd 1997; Milsom et al. 1998), indicating that short vegetation provides superior foraging conditions. The abundance of some prey species has been found to increase with vegetation height (McCracken et al. 1995) and therefore it is thought that short vegetation in general increases the accessibility rather than the abundance of invertebrate food. For example, adult curlew foraging efficiency was observed to reduce as sward height increased (Milsom et al. 1998). The proximal explanation for the increase in accessibility of prey at shorter vegetation heights is not fully understood but may be due to elevated prey detection, increased ease of mobility or it may result from reduced time spent scanning for predators (Devereux et al. 2004). The accessibility of food is likely to be of particular importance to chicks. Lapwing chicks have been found to forage more efficiently in short vegetation (Devereux et al. 2004), and adult Lapwing seen to move their families to areas of short vegetation (Galbraith 1988). Devereux's study found no difference in invertebrate abundance by sward height and so the observed difference in foraging efficiency could be attributed to prey accessibility. Even species that choose to put their nests in longer vegetation often do not choose areas of uniformly tall or dense vegetation, opting rather for a heterogeneous environment with areas of short vegetation, potentially as these could be used for chick foraging (Vickery et al. 2001). The dominant grass species on pasture areas in St Helena is Kikuyu grass *Pennisetum clandestinum*, which forms a dense springy sward that may restrict food availability for

chicks. This is perhaps one reason that habitat suitability declines at high levels of grass cover.

Tall, or thick vegetation in the vicinity of the nest functions both as concealment from predators and as an obstruction to visibility, and therefore predator detection (Whittingham and Evans 2004). Amat and Masero (2004b) found that detection of potential predators (humans) was slower for Kentish plovers nesting near cover compared to those nesting in the open. This has led to two divergent nesting strategies amongst waders. Species such as snipe and redshank opt to have nests in dense taller vegetation and rely upon camouflage to avoid predation. Whereas other species, like the northern lapwing and stone curlew prefer short sward for nesting to maximise visibility and predator detection (Colwell and Dodd 1997; Galbraith 1988). It would appear that the St. Helena Plover fits into the latter category. The plovers also cover their nest when disturbed and therefore early predator detection may allow them to hide their eggs before they themselves are detected. Koivula and Rönkä (1998) consider early flushing behaviour to be an effective adaptation against terrestrial nest predators that hunt using olfaction, as nests without parent birds at them are difficult to find. This would indicate that it would be a successful strategy on St Helena as the main nest predators of the plovers are cats and rats (Burns 2011, Chapter 2). Visibility from the nest may also be one of the reasons that St. Helena Plovers were found to avoid areas with a high percentage cover of shrubs. Alternatively (or in addition), large areas of shrubs may be detrimental as they are likely to support rat populations. Although from an evolutionary perspective rats and cats are recent additions to the fauna of St Helena, the taxon from which the St. Helena Plover arose is like to have been exposed to mammalian predators during its evolutionary history in continental Africa.

The importance of vegetation height and shrub cover to the plovers was emphasised by the results of the change over time analysis. There was still considerable unexplained variation around the regression line using either vegetation parameters or HSI as explanatory variables. This may be partly because birds do not respond instantly to a change in habitat conditions and because habitat change does not act on whole fields, but it does suggest that there are additional factors also influencing population size. Although modelling change in population numbers in relation to congruent change in aspects of the habitat, or an overall estimate of habitat suitability, provides a more

powerful test of causation (Norris 2004), few studies have conducted this analysis (Green 1996; Norris et al. 1998). Norris (1998) found a similar relationship of change in vegetation height over time explaining change in Redshank densities. In this case the increase in vegetation height was directly associated with a reduction in grazing pressure. The HSI was not a better predictor of change in bird density although it is a culmination of all the habitat parameters. This could be because the HSI is based on presence data rather than densities, and also because it represents a general model of suitability across all areas of the island rather than those conditions present at Deadwood Plain. The smallest fields at Deadwood Plain, those less than 4 hectares, were less informative in the change analysis and tended to produce outliers. This may be because the habitat variables in these fields were assessed from a small number of quadrats; additionally since these areas only support a small number of birds there is a large proportionate change in bird density from an increase or decrease of a single pair.

Elevation was the most important parameters determining habitat suitability in the MaxEnt model. Guisan and Zimmermann (2000) described three categories of environmental variables: resource, direct and indirect. Elevation is an example of an indirect variable as it is unlikely to directly influence the suitability of a habitat; rather elevation itself is correlated with one or more parameters that influence suitability. However, indirect measures are often used in habitat models as they are usually the easiest to measure accurately and often are strongly correlated with species distributions. The shape of the relationship between suitability and elevation is likely in part to reflect variation in rainfall and climatic conditions in general, setting the lower and upper bounds of suitability. However it may also reflect the difference in elevation between the two habitat types. The range of elevations over which suitability is increasing are those at which the dominant habitat type is semi-desert (280 – 400 m; Fig. 3, Table 2), and those elevations where the relationship with suitability is more stable are associated with pasture (400 – 600 m), which may indicate that elevation is of greater importance in determining suitability in the semi-desert rather than pasture areas. Habitat associations for the St. Helena Plover in the semi-desert have previously been difficult to discern (McCulloch 2009). One potential correlate of elevation in the semi-desert that may determine suitability is the density of nest predators, in particular rats. Plovers do not appear to distribute themselves within areas of low predator populations on a large scale such as the site-level (FB *pers obs*); however they may be

doing so on a smaller scale. Many of the lower elevation areas in the semi-desert are at the bottom of narrow valleys. These areas will experience a different microclimate to plateau areas and are likely to support more extensive vegetation and therefore they are likely to contain higher densities of rodents. Other species have been observed to choose nest sites dependent on predator densities (Forstmeier and Weiss 2004; Lima 2009; Lima and Valone 1991).

Several studies have found that breeding waders prefer flat areas or those with only a slight slope (Beauvais and Smith 2003; Stillman and Brown 1994). A study of Golden Plover found that nests on sloping areas had lower survival. They inferred that those birds nesting on slopes had less effective anti-predator behaviour (Whittingham et al. 2002), which could have been due to variation in individual quality or reduced visibility on sloping ground. The hypothesis of maximising visibility was also put forward for Mountain Plovers, which have been found to nest on flat areas away from cliffs or other structures (Beauvais and Smith 2003). In St Helena the semi-desert areas at low elevation are also generally steeply sloping and therefore may have reduced visibility from the nest, which may be another reason why they are avoided. In St Helena much of the ground is steeply sloping and therefore the propensity to choose flat areas for nesting may limit the potential to bring currently unsuitable areas into suitable condition.

#### *Nest survival*

In our study we did not find any habitat associations with nest survival. Although some studies have found habitat characteristics to correlate with nest survival or other measures of productivity (Hatchwell et al. 1996; Ricklefs 1969), many have not (Amat and Masero 2004b; Knetter et al. 2002), or have found results to be variable between years (McCulloch and Norris 2002; Prindiville Gaines and Ryan 1988). One compelling reason for this is that if habitats have been chosen by the birds to minimise the risk of nest predation and sufficient area of this habitat is present, then the observed range of habitat variables within territories will be small and will encompass the values which lead to the lowest risk of nest predation. This does not mean that habitat will not have an influence on productivity; however, experimental habitat manipulations are likely to be more successful at detecting these relationships than observational studies.

### *Area of suitable habitat*

The proportion of each site classified as currently being suitable for breeding territories ranged from less than 1 % to 47 %, totalling 275 ha. The current population within the survey sites is 181 birds (SHNT 2011). Therefore, if we estimate the average size of a plover territory as 1 hectare (McCulloch 1992) then the available suitable area appears to be more than sufficient to support the current population. However, as the model shows the maximum potential suitable habitat, it should be regarded as an upper estimate, and therefore actual carrying capacity may be considerably lower.

Additionally, we have calculated the total area of suitable habitat, and have not considered patch size or spatial distribution. Some areas of otherwise suitable habitat may be too small to support a territory. Even if the patch size exceeds that required for a breeding territory, small areas may be less attractive due to the proximity to areas of unsuitable habitat or because they would prevent the aggregation of territories. There may also be other factors that would reduce the attractiveness of potentially suitable areas that were not considered here, for instance, disturbance levels, prey availability or small scale topographic variation. In each site, although it is likely that the density of territories in suitable areas could be increased, there appear to be no large areas of suitable habitat that are totally unused. Whether increasing the area of suitable habitat would be beneficial to the species depends on whether the current area is limiting the population. Given our approximate estimate here it would indicate that the area of suitable habitat is not currently limiting the population. However the population is currently very small and therefore if population size was increased by conservation measures (in order to reduce its vulnerability to stochastic events) then the area of suitable habitat may become limiting at a later date. Habitat availability will therefore be an important parameter to consider when designing conservation management for this species. One potential drawback to our study is that we considered habitat characteristics within current territories only; however the surrounding area may also influence suitability. Several studies have found associations with larger scale environmental parameters for instance distance to roads (Pearce-Higgins et al. 2009), or the extent of enclosure around field boundaries (Milsom et al. 2000). For instance St. Helena Plovers may be nesting in suitable habitat but if they are surrounded by habitat that supports high rodent populations, scrub vegetation for example, then the overall area may actually be unsuitable. If this were the case it would indicate that the area of suitable habitat should be larger than the sum area of territories.

### *Constraints of the habitat suitability model*

At present the model does not tell us which parts of the currently unsuitable habitat could be improved to territory quality, as some will be intrinsically unsuitable. However, we could get an indication of these by plotting those areas with unsuitable topography, as this cannot be altered. The model also cannot account for any time lag between habitat degradation and alteration of the species distribution. This time lag could be exacerbated if species have limited adult dispersal, or if there is a strong tendency for young birds to set up territories where conspecifics are already present, both of which are true in the case of the St. Helena Plovers. Although we have endeavoured to include variables that we assessed to be biologically meaningful in the habitat suitability model, there may be important parameters that were not considered. One aspect that we did not address was a measure how heterogeneous the environment was. Several authors have suggested increasing habitat heterogeneity in pasture areas as a general way to improve nesting and foraging conditions for birds (Benton et al. 2003; Whittingham and Evans 2004). For example if a mix of both long and short vegetation was created on a small scale the long areas may act as a source of invertebrate prey that would be accessible to birds in the shorter areas.

### *Conclusions and management recommendations*

Elevation, vegetation height, slope, shrub cover, and grass cover were found to be the most important determinants of the distribution of the St. Helena Plover. The importance of these three vegetation parameters was emphasised by our change analysis, which showed significant correlation between changes in these parameters and change over time of bird density. It is likely that elevation is an indirect predictor of distribution and it is possible that predator density correlates with elevation in the semi-desert and is influencing habitat suitability. These habitat associations taken together suggest that the St. Helena Plover is trying to maximise visibility around the nest to allow early detection of potential predators. The accessibility of invertebrate prey is also likely to be higher in selected habitats. This leads to direct recommendations for habitat management. In the pasture areas grazing should be sufficient to ensure that grass height and shrub cover are kept low. In the semi-desert the picture is less clear, there appears to be a negative correlation with tall vegetation so reducing the cover of tall invasive species such as prickly pear *Opuntia spp.* may be advantageous. Further



work should investigate potential correlates of elevation that could be directly influencing habitat suitability.

Habitat change explains some of the recent changes in the distribution of the plovers, however it is likely that other variables are also important. Unfortunately, there is no information on recent trends in predator populations; although the popular view of local people is that both feral cats and rodents have increased in recent years. These two parameters, habitat composition and predator densities, are likely to interact as more overgrown vegetation promotes the growth of rodent populations which in turn support higher cat numbers. An interesting avenue of investigation would be to experimentally manipulate habitat within and surrounding current plover nesting sites and investigate the response of both the predator populations and of the plovers. Habitat associations appear to influence primarily the distribution rather than the demography of the St. Helena Plover; however this analysis was limited as we investigated correlates of demography only over the observed range of habitat variables within territories. The area of suitable habitat estimated at present appears to be sufficient to support the current population. However, the aim of conservation management for this species is to increase the population size and so habitat may become limiting in the future.

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## **Chapter 4: Sex differences in behaviour, but not mortality risk, in a critically endangered shorebird**

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### *Author's contributions*

FB: Data collection, statistical analysis, manuscript preparation

NM: Manuscript improvement

NdR: Molecular sexing

MB: Manuscript improvement

TS: Manuscript improvement

## **Abstract**

Sex ratios and sex specific demography are of conservation importance. They influence calculations of effective population size and population growth rate, and can therefore affect estimates of the degree of species endangerment, its potential for recovery, or the optimal management necessary to achieve that recovery. However, for monomorphic species we cannot assess these parameters using traditional methods. We therefore used molecular markers to sex adult and juvenile St. Helena Plovers in order to assess whether demographic rates were sex specific and whether the chick sex ratio was biased. Sex ratio was not different from 50: 50, and neither growth nor survival of chicks was sex-specific, nor did these parameters vary between the two habitats present. Male plovers incubated the nest mostly at night, and this period coincided with the activity of most nest predators. Nevertheless, adult males did not suffer higher mortality as a result; although adult survival was found to vary spatially. These findings suggest that the adult sex ratio is not biased in the St. Helena plover. Additionally our results indicate that this island endemic species has retained anti-predators behaviours that are effective against introduced predators. Our study furthers understanding of this little known species' ecology, allowing us to more accurately assess its population dynamics and understand the threats it faces. Furthermore, the observed variation in adult survival indicates potential for increase, which could dramatically alter the population's potential for recovery.

## Introduction

Sex allocation and sex ratios are amongst the most rapidly advancing fields in evolutionary biology, stimulating a large body of theoretical work (Charnov 1982; Fisher 1930; Frank 1990; Hamilton 1967; Trivers and Willard 1973). Empirical research has largely focussed on the ability or otherwise of species to adaptively modify the primary (at laying) or secondary (at hatching) sex ratios (reviews for birds, Sheldon 1998; West et al. 2002). If there is variation in the parental investment required to successfully raise offspring of either sex, or variation in the reproductive potential of males and females, then it can be adaptive for females to manipulate the sex ratio of their offspring. The optimal sex ratio may be influenced by female condition, and thus her ability to invest, or by environmental parameters, such as the availability of territories or climatic conditions; all of which may interact with each other (Clout et al. 2002a; Komdeur et al. 1997). Parents may also influence tertiary sex ratio (at fledging) by variation in the level of care given, however, in many cases survival to maturation will be strongly influenced by environmental conditions (Nager et al. 2000; Székely et al. 2004). Less work has, however, focussed on the sex ratio of adults. A recent review (Donald 2007) showed that adult sex ratio (ASR) was generally skewed towards males amongst birds and females in mammals. The source of male bias in adult birds was found to be primarily due to higher female mortality rather than skewed offspring sex ratio. Although the proximate causes are not well understood, differential survival between males and females is not unexpected as sexes can have very different ecological requirements, which may vary depending on age or reproductive stage. For instance, many species have sex-specific migration patterns and foraging locations (Catry et al. 2005; Lewis et al. 2002; Verhulst et al. 2004), different energetic requirements (Clutton-Brock et al. 1985; Kalmbach et al. 2009) or different involvement in care of the young (Gruebler et al. 2008), all of which influence their demography.

There are various reasons why understanding the patterns of, and reasons underlying, sex ratios and sex specific demography could be useful to species conservation. To date, however, the extent of theoretical work has not been reflected in its application within conservation projects. Differential survival can influence the effective population size and therefore the population growth rate, thus influencing our estimation



of the level of threat a population is under. For example Gruebler et al. (2008) found that a population of Eurasian Whinchat's *Saxicola rubetra*, was declining 1.7 times faster than anticipated because adult mortality was affecting females more strongly than males. Differential survival may lead to a skewed adult sex ratio which could affect the ability of a population to recover from a low, in particular if males are over-represented (Bessa-Gomes et al. 2004; Durell et al. 2001). This is of particular concern for bird conservation as Donald's review (2007) found that male bias in bird populations increased with conservation threat category. An understanding of sex specific traits can also offer us a greater understanding of the population dynamics of a species and therefore our ability to model it and make robust predictions about its response to perturbations (Coulson et al. 2001a). Finally, an understanding of the role of sex specific traits in regulating populations may allow more effective conservation management plans to be developed (Clout et al. 2002b; Linklater 2003; Verhulst et al. 2004; Wedekind 2002).

Detecting sex-biased mortality is challenging in sexually monomorphic species, since simple morphological traits cannot be used to distinguish sexes. Molecular markers, however, are now readily available for a large number of organisms, and these markers can reliably identify males and females (Dos Remedios et al. 2010; Ellegren 1996; Griffiths and Tiwari 1993). We use molecular markers to sex juvenile and adult St. Helena plovers *Charadrius sanctaehelenae*, a Critically Endangered (BirdLife International 2009; McCulloch 2009) wader, endemic to the isolated Atlantic island of St Helena (15 58'S, 5 43'W). Adults and chicks of this species are monomorphic and thus far there has been no reliable way to sex them in the field.

We had three objectives in this study: Firstly, to investigate the secondary sex ratio and to test whether this deviates from a binomial distribution. Secondly, to investigate whether size at hatching, growth rate, chick survival or the survival of juveniles or adults differ between the sexes. Thirdly, to investigate the behaviour of adult males and females during incubation. The latter issue is of conservation importance, since the probability of predation on nests and possibly on adults is higher during the night (Burns 2011, Chapter 2).

## Methods

St. Helena Plovers, also known as Wirebirds, are present in two major habitat types on St Helena: semi-desert and pasture. Although both habitats are extensively anthropogenically altered, the semi-desert reflects more closely the assumed historic habitat of the plovers prior to human arrival in 1502 (McCulloch and Norris 2001). Five study sites were selected to give a representative coverage of habitat types and geographical range, collectively these sites hold around half the global St. Helena Plover population (see Burns 2011, Chapter 2 for a map showing the location of these sites). Sites selected were Deadwood Plain, Broad Bottom, Man and Horse, Upper Prosperous Bay and Prosperous Bay Plain. The first three sites are predominately pasture and the latter two semi-desert. Few birds were observed at Prosperous Bay Plain, and as the two semi-desert sites are contiguous, data from them were pooled and referred to as Prosperous Bay. St. Helena Plovers are insectivorous, and total invertebrate abundance has been shown to differ between habitats and seasonally, with abundances higher on pasture compared to semi-desert (for a fuller introduction to the species and study sites see McCulloch 1991; McCulloch 1992; McCulloch and Norris 2002). Since many of the parameters investigated in this study could potentially vary between habitats and sites, all analyses have included site or habitat as an explanatory factor, as sample size allows. Variation at the level of habitat or site could potentially be very informative for conservation, additionally controlling for it will allow any influence of sex to be seen more clearly.

Field work was carried out during 2007 – 2009 in two field seasons both spanning November to February; referred to as field season one and two respectively. Throughout field work plover families were observed and the fate of their nests and broods determined. Adult plovers were caught at the nest using either a walk-in funnel trap (Székely et al. 2007b) or a Potter trap, modified after Bub (1978), and chicks were caught by hand. Once captured, birds were ringed and measured (details of ringing protocol can be found in Burns et al. 2010). Chicks were given a uniquely numbered British Trust for Ornithology metal ring at hatching and colour ringed at around two weeks, at which point they were re-measured in order to estimate growth rate. During field season one, chicks were occasionally measured on up to three occasions. Chicks were not recaptured more frequently as it has been shown that frequent capture can

impair survival in a similar species (Sharpe et al. 2009). During field season two, blood samples, ~25  $\mu$ L, were taken at the time of capture for molecular sexing, following guidance in Szekely et al. (2007b). In total 56 chicks and 67 adults were sexed, 41 adults using blood samples and 37 by observation of mating behaviour or through having a mate of known sex. Eleven individuals were sexed using both methods with agreement in all cases. DNA was extracted from samples using the Ammonium Acetate extraction method (Richardson et al. 2001). For molecular sex-typing, CHD-Z and CHD-W genes were amplified via the Polymerase chain reaction using the P2/P8 primers (Griffiths et al. 1998). For additional certainty in sex assignment, the Z-002B/Z-002D primers (Dawson et al., unpublished data) were utilised. IR Dye-labelled tailed primers separated the product of Z-002B/Z-002D and P2/P8 primers into one (ZZ) or two bands (ZW), indicating male or female respectively.

Chick growth was investigated using general mixed models to account for repeated measurements on each chick and non-independence of chicks within a brood. One measure of structural size (bill to feathers) and one measure of condition (weight) were used as response variables. Bill length was chosen as it was thought to exhibit less sampling error compared to tarsus length. Sex, habitat, chick age and a binary factor coding for whether a chick fledged or not were variously used as fixed explanatory variables, see Table 1 for full details of models. Explanatory variables were tested separately to maximise the sample size in each case. The sample was biased towards younger chicks due to chick mortality prior to fledging. Therefore, for models (b) and (c) a proportion of records below the median of the response variable were removed to balance the sample size about the midrange. Box-Cox tests were used to find the most appropriate transformation for the response variable in each model. Models were structured in this way rather than using growth rate as the response variable for two reasons. Firstly, not all birds were measured on more than one occasion therefore estimating growth rate would reduce the sample size. Secondly, the method chosen allows both the size at hatching and the rate of increase to be estimated in a single analysis. However, this model structure does not allow us to test whether growth rate varies with other potential explanatory variables, such a hatch date. In order to estimate survival to fledging, broods were checked approximately every four days; resighting intervals were even between habitats. The ages of chicks found after hatching were

predicted from a non linear regression of known age chicks using bill length as the explanatory variable.

Survival analysis used mixed effects Cox regression models to account for non-independence of chicks within a brood. Our aim here was not to make the most robust prediction of absolute values of chick survival, rather to investigate differences in survival between groups. The response variable was the Kaplan – Meier survival vector, giving age at death and censored status. Age at death was taken as age at the first visit where a chick was not observed. Age at death is unknown for those individuals that survived to fledging or were of unknown fate so these chicks were censored. Chicks that survived to at least 30 days were assumed to have fledged and were given an age of 30. Given variation in the fledging period and the time between site visits this cut-off was set slightly lower than the average time to fledging, which is estimated to be 36 days (Burns 2011, Chapter 6). For chicks of unknown fate, primarily chicks hatched late in the field season, age at last observation was used. The explanatory variables were habitat and the day of the season they hatched. The analysis was repeated using only fully sexed broods with the explanatory variable of sex only.

Two aspects of adult incubation behaviour were investigated, ease of capture and incubation routines. A sex bias in either of these parameters could lead to differential survival if one sex has a greater incentive to return to the nest, or if the timing of incubation matches the pattern of nest predation and therefore the activity patterns of predators. Specifically, it has been found previously that the majority of nest predators are nocturnal and that ~85 % (16/19) of recorded nest predation events occur at night, between 8.30 pm and 4 am (Burns 2011, Chapter 2). Ease of capture was investigated using the time taken for birds to enter the trap, and by looking to see if one sex was caught more often, or first of a pair. Incubation routines were investigated by scoring behaviour continuously from nest camera footage. If an activity occurred for less than 10 seconds it was not recorded. Seven 24 hour periods were recorded from five nests where the sexes could be identified. Sunrise and sunset times were taken as an average of those over the period of video recordings from:

<http://www.timeanddate.com/worldclock/sunrise.html>. Incubation duration was square root transformed and a null mixed model was used with the difference between male and female duration as the response variable and nest identity as the random factor.

This gave an estimate of the intercept only and tested whether this differed significantly from zero. This was done for the full 24 hour period, the day and the night separately. This analysis is equivalent of a paired t-test but takes into consideration multiple samples at some nests. Unless otherwise stated analysis was carried out using R (R Core Development Team 2004).

Annual apparent survival ( $\phi$ ) and resighting probability ( $p$ ) for adults and juveniles were estimated using programme MARK (White and Burnham 1999), including all birds ringed over the two field seasons. The reciprocal of apparent survival is the sum of mortality and permanent emigration. For St. Helena Plovers the latter is likely to be very small as they do not disperse from the island and resighting was carried out at all known plover breeding sites and foraging sites. Resighting was carried out on five occasions: November 2008, February 2009, August 2009, October 2009 and January-February 2010. Due to the irregular spacing and frequency of the resighting periods modelling was done on a monthly basis. Only juveniles that were known to have fledged were included in MARK modelling in order to differentiate between chick survival and juvenile survival; the latter taken as survival from fledging to one year. All models were constant over time as it was felt that the study was of too short duration to be able to detect temporal variation in estimates. The general model was of the form  $\phi p$  (site), for adults and  $\phi p$  (site\*age) for juveniles. Site was a categorical variable indicating the site where a bird was ringed. Levels of site were the four core study sites and Other (O), including all birds ringed elsewhere. Age was used to separate juvenile survival from survival from age one to age two. Sample size for some factor levels of site were small for juveniles and therefore were pooled even in the full model (B, M, and O). All models included different estimates for adults and juveniles and therefore the best fit for juveniles was found first and then this was used for all further models simplifying adult terms. Goodness of fit (GOF) testing was done using a parametric bootstrap. The variance inflation factor  $\hat{c}$  was estimated using the mean of the three methods for its calculation and model selection was adjusted based on the value of  $\hat{c}$  calculated. Second year birds were pooled with adults to test whether these groups had different  $\phi$  or  $p$ . Due to a bias in ringing, the majority of two year old birds were from Deadwood Plain, therefore second year birds were pooled with Deadwood adults. Further model selection was based on an iterative process of collapsing and re-expanding factor levels based on the output of the general model. Model averaging was

undertaken when models were within 2 AIC units of the most parsimonious model. Analysis was repeated using only known sex birds. It was assumed that sex would not influence resighting probability as adults are very site faithful between years and foraging flocks are of mixed sex, and therefore the most parsimonious resighting term from the full dataset was used in all sex specific models. The most parsimonious model from the full dataset was used as the general model, and the influence of sex investigated.

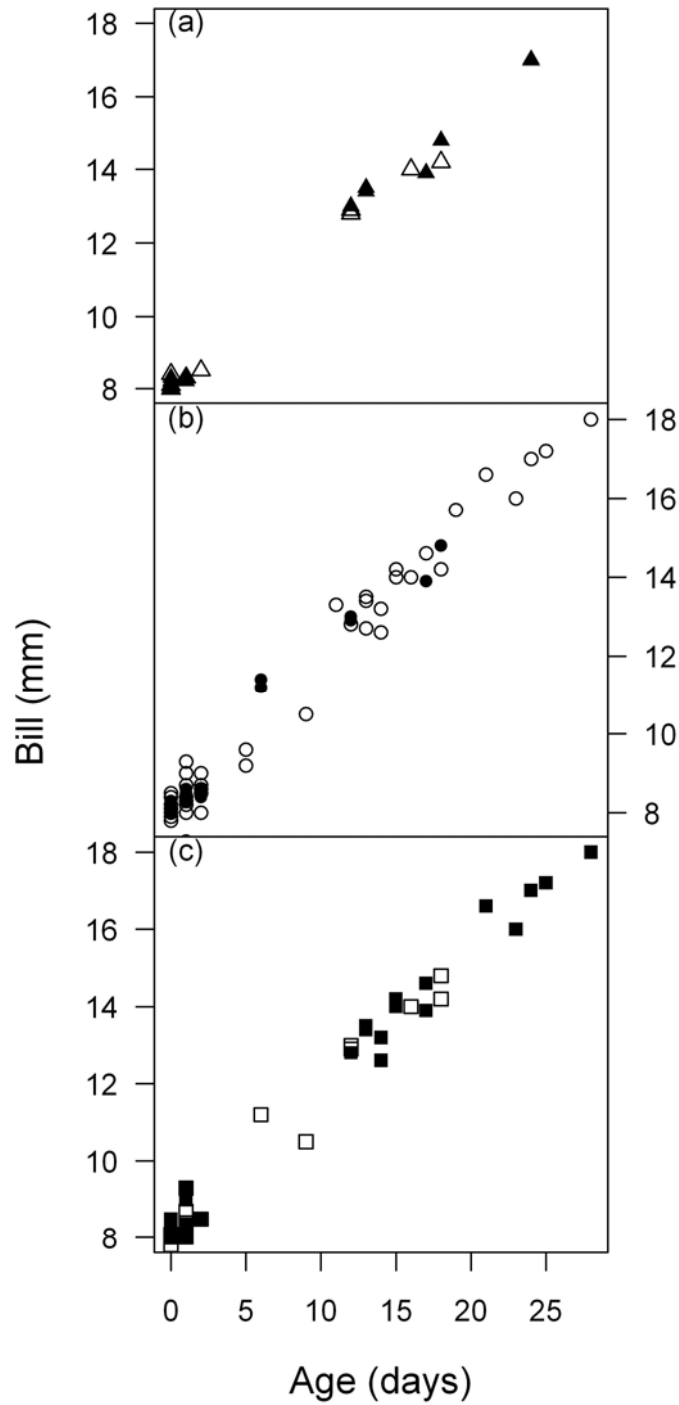
## **Results**

### *Chick sex ratio, growth and survival*

For fully sexed broods, the proportion of male chicks at hatching (N = 16 broods) was not different from expected (0.5, binomial test (19 and 32)  $P = 0.594$ ). The number of male chicks in a brood did not differ significantly from binomial distribution using 0.5 expectation ( $X^2_2 = 1.985$ ,  $P = 0.3706$ ). Model (a) Table 1 investigates the influence of sex on chick growth. As anticipated chick age accurately predicts bill size. However, the intercepts do not differ between the sexes indicating their size does not differ at hatching. The interaction between age and sex is also not significant, showing the rate of increase in bill size with age, in other words the growth rate, does not differ between sexes. Model (b) investigates the influence of the two habitat types. Here we found a similar result; chicks in both habitats start at, and increase in size similarly. Due to the small sample size of fully sexed broods it was not possible to investigate if there was an interaction between habitat and sex. The final model (c) investigates whether growth rate influences the probability that a chick will eventually fledge or not. There is no suggestion from the plot (Fig1. c) or the model output that size at birth or growth rate influences a chick's chance of fledging.

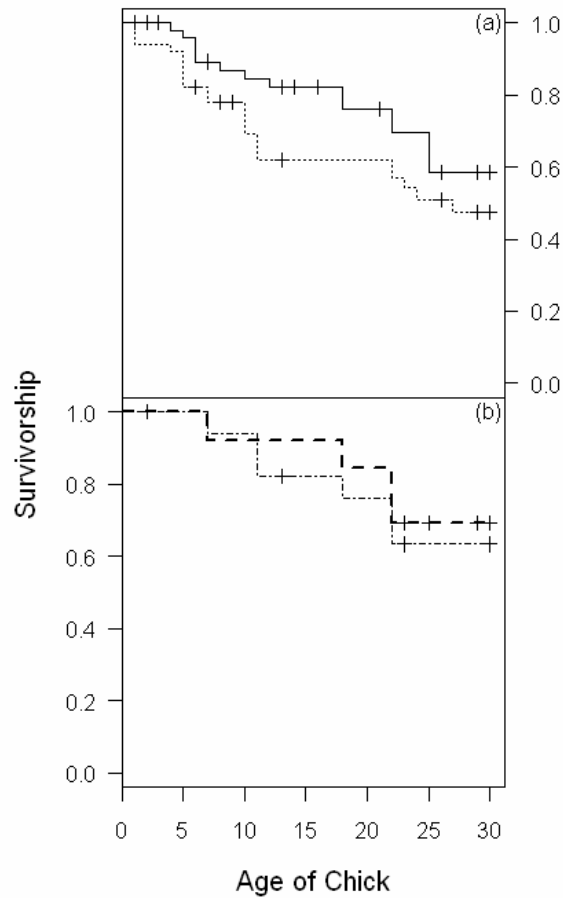
**Table 1** - Mixed models of Chick Growth – models have a nested random effect 1|brood/chick. Year was initially included in models (b) and (c) but showed no significant effects and is therefore not included in the final model; model (a) uses only data from field season 2. Models were also run using weight as the response variable, the results were qualitatively equal.

<i>Hypothesis</i>	<i>Fixed Effects</i>	<i>Estimate</i>	<i>SE</i>	<i>df</i>	<i>T</i>	<i>P</i>
(a) Growth rate varies by sex <i>Obs = 23, chicks = 13</i> <i>broods = 8</i>	Intercept	15.1214	0.3719	8	40.6626	<0.001***
	Age	0.9743	0.03561	8	27.3616	<0.001***
	Sex male	0.1519	0.4709	4	0.3227	0.7631
	Age: sex male	0.05237	0.04350	8	1.2038	0.2631
(b) Growth rate varies by habitat <i>Obs = 42, chicks = 31,</i> <i>broods = 23</i>	Intercept	12.4339	0.3010	20	41.3079	<0.001***
	Age	0.7150	0.02013	8	35.5165	<0.001***
	Habitat semi-desert	0.3800	0.5904	20	0.6436	0.5271
	Age: habitat semi-desert	-0.01265	0.05382	8	-0.2351	0.8200
(c) Growth rate influences the chance of fledging <i>Obs = 36, chicks = 25</i> <i>broods = 17</i>	Intercept	14.04157	0.4049	16	34.6782	<0.001***
	Age	0.8351	0.02496	9	33.4530	<0.001***
	Fate fail	-0.3451	0.5519	7	-0.6253	0.5516
	Age: fate fail	-0.00580	0.04768	9	-0.1217	0.9058



**Figure 1** – (a) Chick growth for each sex, female (open triangles) and male (closed triangles), (b) Chick growth in two habitats, pasture (open circles) and semi-desert (filled circles), (c) Chick growth for chicks that fledged (filled squares) or failed (open squares). Data shown prior to rarification.





**Figure 2** – *Chick Survivorship curves. a) In two habitats, pasture (solid) and semi-desert (dotted), b) for each sex, female (dashed) and male (dot-dash).*

For survival analysis the age of unknown chicks was estimated using a non-linear regression following the Gompertz growth model ( $\text{Age} = 34.00 * \exp(-\exp(3.469 - (0.267 * \text{bill})))$ ;  $R^2 = 0.989$ ). From Figure 2a it appears that semi-desert chicks have lower survival compared to those on pasture, however there is no suggestion that male and female chicks survive differentially (Fig. 2b). The results of the Cox regression for chick survival (Table 2) indicate that whilst there is no significant difference in survival between habitats (model a), there is a significant interaction between habitat and hatch day. Survival in pasture areas does not vary over the season, whereas survival declines over time in the semi-desert. No difference was observed in the survival of male or female chicks (Table 2, model b).

**Table 2** - Cox mixed-effects regression model for chick survival to fledging, all models contained a random effect of brood.

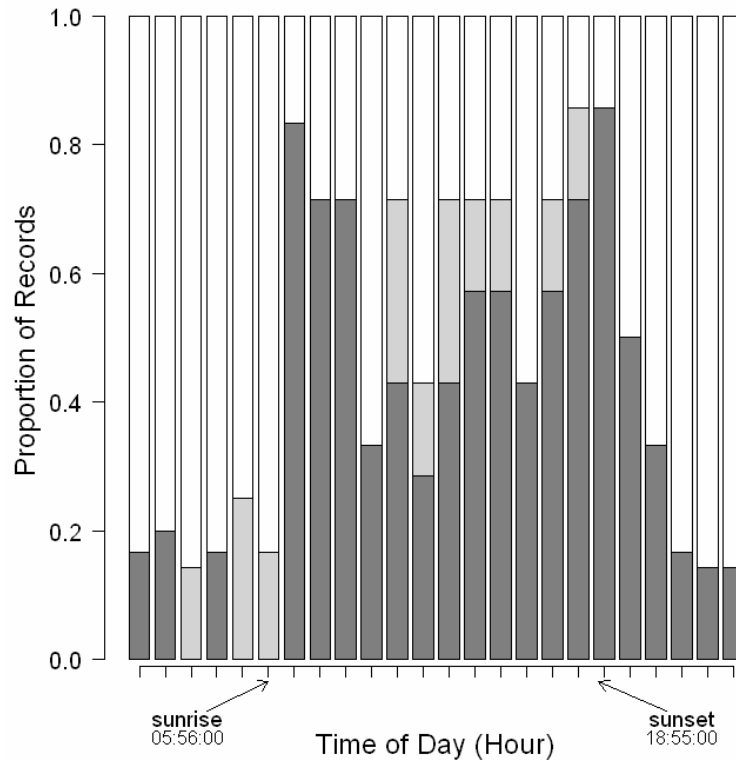
<i>Hypothesis Tested</i>	<i>Response</i>	<i>Fixed Effects</i>	<i>Estimate</i>	<i>SE</i>	<i>Z</i>	<i>P</i>
(a) Survival varies by habitats or seasonally <i>chick = 103, brood = 61</i>	Survival	Habitat semi-desert	-4.0243	2.3745	-1.69	0.09
		Hatch day <sup>1</sup>	-0.01153	0.01810	-0.64	0.52
		Habitat semi-desert : hatch day	0.06457	0.02980	2.17	0.03*
(b) Survival varies by sex, <i>chick = 32, brood = 16</i>	Survival	Sex male	0.07141	0.9923	0.07	0.94

1: The day of the season on which the chick hatched, taking the first day of field work as day one.

#### *Adult incubation behaviour and survival*

Females were more likely to be caught first out of a pair (binomial test (23, 31),  $P = 0.011$ ). Additionally, if only one parent was caught it was more likely to be the female (binomial test (14, 18),  $P = 0.031$ ). An ANCOVA showed that the time taken for the bird to enter the trap was not related to sex ( $F_1^{28} = 0.2714$ ,  $P = 0.6065$ ) or the age of the nest ( $F_1^{28} = 0.2360$ ,  $P = 0.6309$ , interaction  $F_1^{28} = 1.9280$ ,  $P = 0.1759$ ). We therefore investigated whether males and females incubated at different times of the day. The overall daily pattern found (Figure 3) indicates that males do the majority of incubation during the night, that females take over at dawn and dusk, and that there is a more equal sharing during the middle of the day. Over the 24 hour period no difference was found in the contributions of males and females to incubation duties ( $\bar{\varphi} = 0.477$ ,  $SD = 0.124$ ,  $t_5 = 0.195$ ,  $P = 0.853$ ). However, during daylight females did significantly more ( $\bar{\varphi} = 0.649$ ,  $SD = 0.129$ ,  $t_5 = -3.641$ ,  $P = 0.0149$ ). Fig. 3 indicates that the trend during the night is more polarised, with females only doing 24 % of incubation on average. However the trend is not significant when tested ( $\bar{\varphi} = 0.242$ ,  $SD = 0.283$ ,  $t_5 = 1.599$ ,  $P = 0.171$ ), due to the presence of an outlier. This was due to a female bird continuing to incubate well into the evening before being relieved by her partner. A significant trend towards male incubation is seen after the removal of the outlier ( $t_4 = 3.152$ ,  $P = 0.0345$ ). Using the diurnal proportions of time incubating for each sex as the expected values in a chi

squared test indicates that incubation routines can explain the difference in catching frequency between males and females ( $X_1^2 = 1.17$ ,  $P = 0.280$ ).



**Figure 3** – Proportion incubation by female (dark grey) and male (white) *St. Helena Plover*. Light grey indicates neither parent is on the nest (The graph shows what was happening on the hour, each hour, for illustration only.  $N = 7$  nests).

The general model for the full dataset of adult and juvenile survival fitted adequately (GOF testing,  $\hat{c} = 1.04$ ), as did the general model for the known sex dataset (GOF,  $\hat{c} = 1.008$ ). There was little support for models splitting second year birds from older adults (Table 3); therefore in all other models these groups are pooled. Model selection indicated that adult resighting differed between sites, and there was also limited support for differential resighting of juveniles at different sites. Adult survival also differed with site, forming two groups, with Man and Horse and Other categories showing lower survival than the other sites. Additionally, juveniles born at Deadwood Plain had higher survival than those from other areas. There was uncertainty in selecting the most parsimonious model; there were three models within 2 AIC units of the minimum differing only in their juvenile terms. Model averaging for Juvenile survival and

resighting was therefore undertaken; results shown in Table 4. From MARK modelling of the known sex dataset there is no support for models that include sex specific survival for adults or juveniles.

**Table 3** - Model output from programme MARK, showing all models with a weight of over 0.01, and the starting model. All models considered for the known sex dataset are shown. Key: S-site, D-Deadwood Plain, B-Broad Bottom, M-Man and Horse, P-Prosperous Bay, O-Other, R-remainder, C-constant, K-the number of parameters. Group levels combined with a plus have been pooled.

<b>Full dataset</b>				<i>N=108<sub>A</sub>, 72<sub>J</sub></i>			
$\Phi_A$	$\Phi_J$	$p_A$	$p_J$	$\Delta QAIC$	$K$	Deviance	Weight
$S^1_{(R, M+O)}$	$S_{(R,D)}$	$S_{(O, D+P, M+B)}$	C	0	8	272.79	0.295
$S_{(R, M+O)}$	$S_{(R,D)}$	$S_{(O,D+P,M+B)}$	$S_{(R,D)}$	0.32	9	271.03	0.251
$S_{(R, M+O)}$	C	$S_{(O,D+P,M+B)}$	$S_{(R,D)}$	1.02	8	273.81	0.177
$S_{(R, M+O)}$	$S_{(R,D)}$	S	C	2.42	10	271.03	0.088
$S_{(R, M)}$	$S_{(R,D)}$	S	C	2.74	10	271.35	0.075
S	$S_{(R,D)}$	$S_{(O,D+P,M+B)}$	C	3.74	11	270.25	0.045
$S_{(R, M,O)}$	$S_{(R,D)}$	S	C	4.15	11	270.66	0.037
$S^1$	$S_{(O, D, P, Age)}$	S	$S_{(O, D, P, Age)}$	15.24	18	266.76	< 0.001
<b>Known sex dataset</b>				<i>N= 64<sub>A</sub> (26<sub>M</sub>), 34<sub>J</sub> (17<sub>M</sub>)</i>			
$S_{(R, M+O)}^1$	$S_{(R,D)}$	$S_{(O,D+P,M+B)}$	C	0	8	314.60	0.681
$S_{(R,M+O)}$	$S_{((R,D)*Sex)}$			2.85	10	313.21	0.164
$S_{((R,M+O)*Sex)}$	$S_{(R,D)}$			3.40	10	313.76	0.125
$S_{((R,M+O)*Sex)}$	$S_{((R,D)*Sex)}$			6.35	12	312.42	0.029
C	C			13.60	6	332.39	0.001
Sex	C			14.92	7	331.62	< 0.001
C	Sex			15.44	7	332.14	< 0.001
Sex	Sex			16.75	8	331.36	< 0.001

1: Starting models on which GOF testing was done.

**Table 4 - Parameters estimates based on the full dataset.**

<i>Parameter</i>		<i>Monthly <math>\Phi</math> (CI)</i>	<i>Derived <math>\Phi^1</math> (CI)<sup>2</sup></i>
Adult	Man & Horse, Other	0.971 (0.948, 0.984)	0.703 (0.654, 0.741)
	Remainder	0.989 (0.980, 0.994)	0.876 (0.852, 0.894)
Juvenile	Deadwood Plain	0.947 (0.895, 0.974)	0.580 (0.521, 0.642)
	Remainder	0.901 (0.838, 0.941)	0.351 (0.300, 0.406)

1: Annual survival for birds one year or older, or survival from fledging to one year (10 months).

2: The 2.5 and 97.5 percentiles of distribution of 1000 estimates of derived survival, each one the product of 12 estimates of monthly adult survival, or 10 estimates of monthly juvenile survival, randomly chosen from the respective distributions.

## Discussion

Our study observed temporal partitioning of incubation duties between male and female St. Helena Plovers; with male birds incubating during the period of greatest nest predator activity. Nevertheless, this did not translate into a difference in adult mortality between the sexes. Furthermore, no sex related differences were found in the other demographic parameters investigated and chick sex ratio was not biased. These results suggest that adult sex ratio is not biased in this species. Skewed adult sex ratio may suppress population growth rate by reducing the effective population size and may often go unnoticed in monomorphic species.

If chicks of each sex differ in their need for resources or the benefits they accrue from them, and the parent birds or the environment vary in their ability to provide these resources, then it can be adaptive for parents to bias parental investment towards the sex that would benefit most. Some empirical studies have found evidence that supports this (e.g. Appleby et al. 1997; Burley 1981; Komdeur et al. 1997). In shorebirds, recent studies have suggested adaptive bias in primary sex ratio in Ruff *Philomachus pugnax*, Common sandpipers *Actitis hypoleucos* and Kentish Plovers *Charadrius alexandrinus* (Andersson et al. 2003; Székely et al. 2004; Thuman et al. 2003). Our results show no bias in sex ratio at hatching at the population level, and it does not appear that individual females are choosing one sex over the other, as allocation into broods did not differ from random. Our findings conform with the majority as, although possible,

adaptively biasing secondary sex allocation does not appear to be common amongst birds (Ewen et al. 2004). As well as investigating adaptive bias, knowledge of secondary sex ratio is also useful when interpreting the demography and life history of species.

Our results suggest that chick sex and natal habitat do not influence initial chick size or growth rate and that the rate of growth explains little variation in the probability of fledging. Many studies have found differential growth and survival between chicks of different sexes (see examples in Clutton-Brock 1986; Nager et al. 2000; Torres and Drummond 1997). In the majority of cases it is the smaller sex at adulthood, predominately the female, that survives better and it has been hypothesised that the larger male chicks struggle to obtain sufficient food to maintain their higher growth rate, in particular in times of low food availability. Conversely, male Kentish Plovers chicks, the only wader species in which sex specific chick survival has been considered, were found to be larger at hatching, and to grow faster and survive better than females (Székely et al. 1999; Székely et al. 2004). Male adult Kentish Plovers are slightly larger than females, but a similar weight (Küpper 2008), and show dimorphic plumage. Conversely, adult St. Helena Plovers are monomorphic in plumage and biometrics and so it may not be unexpected that their chicks do not show sex specific growth patterns. However, some parameters that have been proposed to explain differential chick growth or survival do not rely upon adult dimorphism, for example, age at recruitment (Daan et al. 1996) or hormonal levels (Müller et al. 2005). It is more surprising perhaps that no difference in growth rate or survival was found between the different habitats; although similar studies of other shorebird chicks have found variable results (Kosztolányi et al. 2007; Loegering and Fraser 1995; Pienkowski 1984; Székely et al. 2004; Thomson 1994). Although neither habitat on St Helena appeared to limit the growth of young plovers, survival did decline throughout the season in the semi-desert and was lower overall, if not significantly so. The reasons for this seasonal decline are not clear, however a short term decline in food supply is possible as invertebrate abundance appears variable within and between years (McCulloch and Norris 2002). Differences in climatic conditions between habitats may also influence chick growth and survival. The time chicks need to be brooded for increases at low temperatures and during extended rainfall and this may restrict chick foraging time (Beintema and Visser 1989; Pearce-Higgins and Yalden 2002). Climatic conditions on St Helena are mild and it is

unlikely that foraging time is compromised by temperature; however chicks may be disadvantaged during extended periods of rain. It is arguable that chicks in the semi-desert are affected more severely, although in general pasture areas are wetter. After extended rain the substrate of the desert becomes difficult to traverse, and chicks have been observed with their feet covered in sufficiently thick layers of dried mud to impede movement. Island average monthly rainfall increases as the field season progresses and this may be one reason for the decline over time in survival in the semi-desert.

In our study neither habitat per se, nor sex appears to be influencing chick growth or survival, however survival remains low. Other studies have cited disturbance as a threat to chick survival (e.g. Lord et al. 2001; Ruhlen et al. 2009). However, disturbance appears unlikely to contribute significantly to chick mortality as plover breeding sites are seldom disturbed by humans, and where livestock are present they are at low densities. A more plausible explanation is that chick survival is limited by predation. Introduced predators are known to be the cause of the vast majority of nest failures, and it is likely that these species are also responsible for chick predation. The slightly lower survival overall in the semi-desert may be explained by the higher density of cats here compared to the most successful pasture site, Deadwood Plain, where many of the pasture chicks originated (Burns 2011, Chapter 2).

Adult mortality is not predicted to differ between sexes due to difference in propensity to return to the nest. However, the survival of male St. Helena Plovers could be compromised as they, like most other male *Charadrius* species, incubate throughout the night (Table 5); which is the active period of most predators on St Helena. Amat & Masero (2004b) found that male Kentish Plovers, which show a similar partitioning of incubation duties, were more likely to be predated at the nest. They attributed this to lower visibility, and therefore poorer escape responses, during the night. Additionally, it has been suggested that the female biased sex ratio of the Stewart island population of the New Zealand dotterel *Charadrius obscurus* developed due to lower male survival during night time incubation (Dowding and Davis 2007). However, whether one or other sex is more at risk will depend on the composition of the local predator community. For instance, the Two-banded Plover *Charadrius falklandicus* shows the standard incubation pattern, however, females may be more at risk as all the nest predations recorded for this species were during the hours of daylight (St Clair et al.

2010a). Additionally, incubation may incur costs other than elevated mortality risk, for example heat stress. Amat and Masero (2004a) found Kentish plovers exhibiting thermoregulatory behaviours at ambient temperatures frequently experienced by St. Helena Plovers.

**Table 5 - Daily Incubation Patterns** – male and female symbols indicate where one sex incubates for a significantly greater proportion of the time period. Equal sign indicates that incubation is shared equally during that time period.

<i>Species</i>	<i>Day</i>	<i>Night</i>	<i>Total Effort</i>	<i>Source</i>
St. Helena Plover	♀	♂	=	This paper
Kentish Plover	♀	♂	♀	(Kosztolányi and Székely 2002a)
Two-banded Plover	♀	♂	=	(St Clair et al. 2010a)
Killdeer <i>C. vociferous</i>	♀ <sup>1</sup>	♂ <sup>1</sup>		(Warnock and Oring 1996)
Rufous-chested Dotterel <i>C. modestus</i>	=	♀	=	(St Clair et al. 2010b)
Golden Plover	♂	♀	=	(Byrkjedal and Thompson 1985)
Ringed Plover	=	=	=	(Wallander 2003)

1: Descriptive data only, no statistics presented.

Juvenile survival is usually difficult to differentiate from natal dispersal. However, since there is no dispersal from St Helena our estimates will reflect survival more closely than other studies. Our results indicate a difference in survival between juveniles hatched at Deadwood Plain and those hatched elsewhere. This could partly be a sampling issue as more chicks were ringed at Deadwood than elsewhere. Indeed, since juvenile birds move around the island in flocks, site or sex specific survival may not be expected. Survival may differ however, if there is substantial competition between young males to gain access to territories or mates. So far sex specific juvenile survival has not been observed in shorebirds, although few studies have investigated the potential (Dinsmore 2008; Sandercock et al. 2005b). Our estimates of juvenile survival (Table 4) are at the higher end of those found for similar species; Piping Plover (0.32, Larson et al. 2000), Snowy Plover *C. alexandrinus* (0.39, Paton 1994), Madagascar



Plover *Charadrius thoracicus* (0.36, Zefania et al. 2008); the latter of which is also a non-migratory island species.

Adult survival was found to be relatively high for St. Helena Plovers, with the overall survival of adults estimated at 83 %. This is similar to estimates for other island dwelling, or non-migratory *Charadrius* species (Lloyd 2008; Zefania et al. 2008) and higher in general than migratory ones (Lloyd 2008; Nol and Blanken 1999; Sandercock 2003). In agreement with our findings little support has been found for sex differences in adult survival in plovers (Larson et al. 2000; Sandercock et al. 2005b), in contrast to other groups of birds where in general females have been found to have lower survival (Coulson and Wooller 1976; Gruebler et al. 2008; Promislow et al. 1992). One reason why the difference in adult survival between the sexes could be lower in shorebirds, compared to birds in general, is that incubation is generally shared by both parents in shorebirds, compared to females only in other taxa. Two studies have found a sex bias in adult survival amongst shorebird species, Semipalmated Sandpiper *Calidris pusilla* and Ringed Plover (Sandercock and Gratto-Trevor 1997; Sandercock et al. 2000; Wallander and Andersson 2003). In both these cases females suffered higher apparent mortality than males, however this was attributed in whole or in part to differential adult dispersal. Female mortality in Semipalmated Sandpipers did appear to be higher than males at the breeding grounds, this is possibly because females incubate at night (Jehl 2009). Adult survival was found to be lower at Man and Horse and for birds not ringed at the core sites. Productivity has also been found to very low at Man and Horse due to high levels of nest predation (Burns 2011, Chapter 2), so it is possible that adults are also experiencing a higher level of predation at this site.

### *Conclusions*

This is the first study to investigate sex specific characteristics in St. Helena Plovers and the sample sizes are sometimes limited, so the results presented here are preliminary. Nevertheless, there are several findings pertinent to conservation. Firstly, no chick sex ratio bias or sex-specific differences in demographic parameters were observed, even though male birds' incubation coincided with the period of greatest nest predator activity. This indicates that St. Helena Plovers have retained effective anti predator behaviour, despite the absence of native nocturnal predators on St Helena; one of the endemic rails may, however, have been an occasional egg eater (Olson 1975). These results also suggest that adult sex ratio does not exhibit the male bias found in other

endangered bird species. This is good news for species conservation as an overabundance of males may suppress the population growth rate through a reduced effective population size. Secondly, the variation observed in adult survival between sites indicates potential for increase in some areas (Table 4). This could greatly benefit population recovery as adult survival is commonly the strongest determinant of population growth in shorebirds (Koivula et al. 2008; Ottvall and Hårdling 2005; Plissner and Haig 2000). Lower survival could, however, be attributable to individual quality, rather than the environment, which would limit the potential for change through conservation management. Thirdly, there was no indication that habitat is influencing the growth or survival of chicks to fledging, allowing us to focus conservation on those parameters that are likely to be limiting chick survival, for instance predation. Nevertheless, only one way in which habitat could be influencing productivity was investigated here. Habitat type could influence the territory size required to raise chicks or specific aspects of each habitat could be affecting chick survival. Future work will investigate these ideas.

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**Chapter 5: More harm than good? Assessing the impact of nest exclosures for the endangered St. Helena Plover *Charadrius sanctaehelenae***

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FB: Data collection, statistical analysis, manuscript preparation

NM: Manuscript improvement

TS: Manuscript improvement

MB: Study design, manuscript improvement

## Abstract

The use of exclosures to protect the eggs of ground nesting birds has become a widespread conservation management technique. Although the exclosures are intended to increase nest survival, the results of studies have been mixed. We conducted a trial of nest exclosures on an endangered small wader, the St. Helena Plover *Charadrius sanctaehelenae*. We found that total incubation time was not affected by the presence of exclosures. However, we found no increase in nest survival in protected nests compared to control ones. Additionally, we recorded an elevated probability of adult mortality associated with exclosures. Cats *Felis catus* are the dominant predator of plover nests and it became clear that exclosures did not exclude all individuals; explaining why nest survival remained unchanged. It is also likely that cats were responsible for the observed adult mortality. We found that even if exclosures had excluded all cats, the benefits of increased nest survival would have been completely negated by the estimated decrease in adult survival and the net population trend poorer overall. Adult mortality associated with nest exclosures has been recorded in several studies of ground nesting birds, and it is therefore essential to assess the overall influence of exclosures on demography.

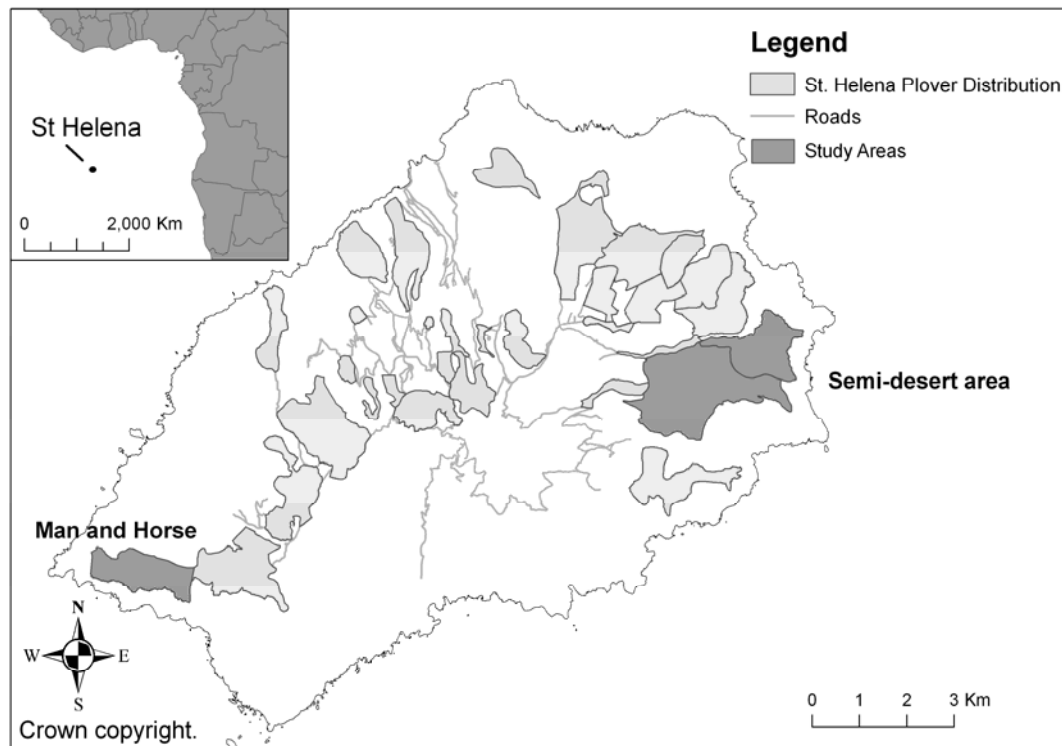
## Introduction

In the last two decades nest exclosures have become a common technique of conservation management for ground nesting birds. A recent meta-analysis has shown the overall effect of nest exclosures on nest survival to be significantly positive (Smith et al. 2011), however the results of individual studies have been mixed (e.g. Mabee and Estelle 2000), and the overall positive result would be negated by the addition of only a small number of currently unpublished, non-significant, results to the analysis. Therefore, carefully controlled trials are required when nest exclosures are being used on a new species or in a new locality.

The St. Helena Plover *Charadrius sanctaehelenae* (also known as the Wirebird) is a small sand plover endemic to the isolated oceanic island of St Helena, South Atlantic (Figure 1). The St. Helena Plover was designated as Critically Endangered in 2007, and although numbers appear to have stabilised, the population remains small, isolated and vulnerable (BirdLife International 2009; McCulloch 2009). The use of nest exclosures was proposed as a short term way to boost productivity whilst more long lasting conservation options were evaluated. Exclosures were chosen as they are straightforward to install and monitor, and therefore can be used after little training. Additionally, they are relatively cheap to produce. Demographic studies also suggested that an increase in nest survival would be advantageous (Burns 2011, Chapter 6). Although nest survival for the St. Helena Plover is within the range of comparable species such as African small plovers (Baudains and Lloyd 2007; Lloyd 2008; Tulp 1998; Zefania et al. 2008), nest success was very low in some areas of the island where it was proposed that exclosures be used (Burns 2011, Chapter 2).

Like other isolated oceanic islands, many species have been introduced to St Helena since its discovery by humans in 1502 (Ashmole and Ashmole 1997). St Helena had no native mammals prior to this date, whereas now invasive mammals make up the majority of terrestrial vertebrate biomass. Recent field studies using nest cameras recorded only introduced species predating St. Helena Plover eggs, with the domestic or feral cat *Felis catus* emerging as the most important nest predator (Burns 2011, Chapter 2). For nest exclosures to be successful there needs to be a substantial size differential between predator and prey species, allowing the exclusion of the predator but easy

access for the parent birds. Cats are larger than the plovers by a sufficient degree for it to be considered that this criterion is met.



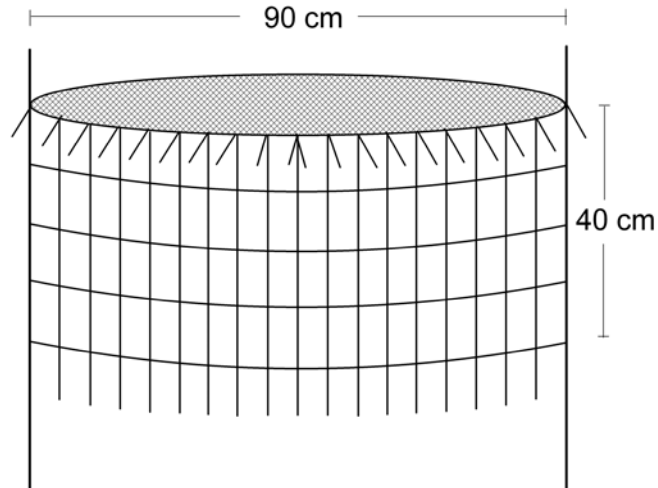
**Figure 1** - St Helena showing the core St. Helena Plover range and the study areas, the location of the island is shown inset

Nest exclosures have the potential to influence demographic parameters other than nest survival. Several studies have investigated the impact of nest exclosures on overall productivity (Cohen et al. 2009; Pauliny et al. 2008) and adult mortality (Table 3). However, few studies so far have looked into the influence of exclosure use on other aspects of the annual cycle. Hardy & Colwell (2008) and Isaksson et al. (2007) investigated parameters such as incubation duration, synchrony of hatching and hatchability. The only difference found was an increase in incubation duration for northern lapwing *Vanellus vanellus* (Isaksson et al. 2007). A possible explanation for this increased incubation period would be a change in the incubation behaviour of one or both parent birds; however no study has so far sought to investigate this possibility. Here, we undertook behavioural observations at all nests to ascertain whether exclosures influence incubation behaviour.

## Methods

The study was carried out on the island of St Helena in the South Atlantic Ocean (15°58'S 5°43'W) between 8<sup>th</sup> January and 2<sup>nd</sup> March 2010. Two areas were initially chosen for the experiment; however, as the study progressed it became clear that nesting success was so low at one site, Man and Horse, that insufficient nests were surviving long enough to be included in the trial. This meant that all but two nests (one in each group, treatment and control) were from the same area; the semi-desert in the east of the island (Fig. 1). A total of 22 nests (eleven in each group) were followed in this latter area. The choice of sites for the study may influence the observed change in daily nest survival from exclosure use. Large site-specific variation in survival of control nests and the exclusion of a potential study area because high rates of nest loss precluded deployment of exclosures could lead to an underestimate of the effectiveness of their benefits across the population as a whole. However, the semi-desert area was a good candidate site, since previous work had shown low rates of nest survival there, and cats were likely to be the most important predator as densities of other small nest predator species, such as the Common Myna *Acridotheres tristis*, were low (Burns 2011, Chapter 2). In addition, the effectiveness of exclosures was modelled at the level of the entire population (see analysis section below).

Exclosures (Figure 2) were formed from a cylinder of PVC coated wire mesh (5 x 10 cm, gauge ~ 2.5 mm) and fitted with a chicken wire roof (2.5 cm square mesh); similar to those used by several other authors (Estelle et al. 1996; Johnson and Oring 2002; Mabee and Estelle 2000). The mesh size was chosen with the aim of excluding cats. The top row of the mesh was threaded through the chicken wire to secure the roof and then bent downwards, as shown in Fig. 2, to prevent animals pushing the structure over or jumping on top of it. The exclosures were 90 cm in diameter and 40 cm tall, with a row of wire mesh spikes, each 8cm long, around the bottom. The spikes were buried and the structure secured with tent pegs. Four metal bars, 0.5 cm thick, were threaded vertically through the mesh and at least 20 cm into the ground to increase the rigidity of the exclosure. A relatively small exclosure diameter was chosen so that one worker (FB) could easily and quickly set them up in a maximum of ten minutes.



**Figure 2** – *Diagram of the enclosure design, showing two of the vertical metal bars at either side. Ground level is equal to the bottom horizontal bar. Vertical bars were 5cm apart.*

Sites were visited approximately every two days. When the first nest was discovered in each sub-area it was randomly allocated to the treatment (enclosed) or the control (no enclosure) group. Thereafter nests were alternately allocated to the respective groups. Enclosures were only erected at nests that had been incubated for approximately one week to minimise the risk of nest abandonment, which has been recorded in some other enclosure studies (Hardy and Colwell 2008; Maslo and Lockwood 2009; Richardson 1999). Nests that failed during the first week of incubation were therefore not included in the study. We predicted the age of nests found after clutch completion from egg measurements using the technique developed by Furness & Furness (1981). An infra-red motion sensitive nest camera was set up at one treatment nest to try to identify nest predators, the design followed that of Bolton (2007).

The behaviour of both parent birds was recorded continuously and separately before and after enclosure installation. If an activity occurred for less than 10 seconds it was not recorded. Observation periods lasted one hour and in general no more than one observation was made at a nest each day. Control nests were monitored for a total of three hours spread over the course of incubation. Treatment nests were observed for at least two hours before enclosure implementation, and for at least three hours subsequently during the lifetime of the nest. This does not include observations taken

during the first hour after exclosure installation, which were excluded from the analysis. The target number of observation hours was not achieved for several nests as they failed before all observations could be undertaken. Observations were undertaken throughout the day to control for daily variation in incubation behaviour, and time of day and air temperature were recorded at the start of each observation. The birds are monomorphic and were not all individually colour ringed so it was not possible to distinguish the identity or sex of the incubating parent.

### *Analysis*

#### Nest survival and incubation

All analysis was carried out in Programme R (R Core Development Team 2004). The two nests from Man and Horse (Fig 1.) were not included in analysis as we could not control for the confounding effect of site identity. However, analyses were repeated including these nests and their inclusion did not alter our general conclusions. The exception to this is when modelling the impact of nest exclosures on the population, see following section for justification. Nest survival was estimated using the Mayfield method (Mayfield 1975) and values were compared using a Z statistic as described in Johnson (1979). Several other parameters are commonly found to influence nest survival, in particular nest age and time within the breeding season. However, due to the moderate sample size in our study we could not investigate these influences. Nevertheless, since experimental design was balanced throughout the duration of the study and since the average age at finding did not differ between the experimental groups it is thought that the inclusion of these parameters would not qualitatively alter our conclusions.

Incubation behaviour was investigated using generalised linear mixed models with binomial errors. The response variable was the proportion of the hour-long observation during which the nest was incubated, hereafter referred to as total incubation time. Stage (pre- or post implementation) or group (control or treatment), the age of the nest when the observation was undertaken, the number of days since the start of the field season and ambient temperature (linear and quadratic), were fixed effects and nest identity was a random factor. A quadratic effect of temperature was included as increased nest attendance can be required at both high and low extremes of temperature, to shade or warm eggs respectively. Although time of day was recorded it was strongly



correlated with temperature and therefore was not used. First order interaction terms were included where it was judged they expressed a meaningful hypothesis. Since the data were non-orthogonal the order of removal of terms from the full model mattered. Therefore, all possible permutations of model simplification were calculated, first for the interaction terms and then the main effects, and the minimum adequate model (MAM) was chosen as that only containing significant effects; all deletion routes led to the same MAM.

### Modelling the impact of nest exclosures

Since an increase in adult mortality associated with nest exclosures has previously been observed (Table 3), all nests (control and treatment) were closely monitored so that any similar trend in our study system would be quickly detected. Unfortunately, elevated adult mortality was observed to be associated with exclosures (see results; Table 3). In order to investigate the impact of this increased adult mortality on the ability of nest exclosures to benefit the population, the combination of adult survival ( $S_A$ ) and nest survival ( $S_n$ ) that would lead to a stable population (assuming other vital rates remain unaffected) was plotted. Nest survival is the chance of a nest hatching at least one egg. For this simulation all individuals were considered equal and genetically monogamous. Population size ( $N$ ) in future years depends on the balance between the number of adults dying and the number of juveniles being recruited into the adult population. The number of recruits is calculated from several further parameters (Equation 1): brood survival ( $S_B$ ), chance of at least one chick fledging from a brood, the average number of chicks fledged in successful broods ( $C_B$ ), juvenile survival ( $S_J$ ), the chance of survival from fledging until one year old, and nests pair<sup>-1</sup> year<sup>-1</sup> ( $N_P$ ). The resulting estimate must be divided by two as recruits are produced per pair rather than per individual. The values used in this analysis are the average ones found from ongoing research across four St. Helena Plover populations, (Burns 2011, Chapter 2, 4, 6) shown in Appendix 1.

$$N_{t+1} = N_t - (deaths) + (recruits)$$

$$deaths = N_t (1 - S_A)$$

$$recruits = \frac{N_t S_n S_B C_B S_J N_P}{2} \quad \text{Equation 1}$$

Assuming a stable population and unbiased sex ratio, we can predict  $S_A$  from Equation 2.

$$S_A = 1 - \left( \frac{S_n S_B C_B S_J N_P}{2} \right) \quad \text{Equation 2}$$

In relation to the predicted stable population, three scenarios were investigated;

- i) Baseline of observed  $S_A$  and  $S_n$ ;
- ii) The potential increase in  $S_n$  from exclosure use, assuming  $S_A$  remains unchanged;
- iii) Both the potential increase in  $S_n$  and the concurrent observed decrease in  $S_A$ .

The estimated increase in  $S_n$  assumes that the exclosures effectively excluded cats (which are responsible for 65 % of nest predation (Burns 2011, Chapter 2)) and that exclosures are used on half of nests (a (65 % \* 50 %) reduction in daily nest failure rate), increasing nest survival from 21.48 % to 35.72 %. For the purposes of this simulation predation is assumed to be responsible for all nest failures, and therefore daily predation pressure is one minus daily nest survival.

In order to make a conservative estimate of the increase in adult mortality, all nests protected in the study were included here, including the one from Man and Horse; giving twelve nests in total. The estimated decrease in  $S_A$  is extrapolated from two adults predated out of the 24 parent birds at the twelve protected nests, and assumes that nests pair<sup>-1</sup> year<sup>-1</sup> remains constant at 2.48 (Burns 2011, Chapter 6). If we assume that half the nests are enclosed, each pair on average has 1.25 nests protected, giving an increase in adult mortality of 10.42 %. This mortality is assumed to be additive to existing adult mortality as no adult mortality was associated with any of the control nests, and thus reduces annual adult survival from 82.92 % to 72.50 %. Since the area around all nests was carefully searched for evidence of adult mortality it is unlikely that any adults deaths were missed, however, since not all the birds are uniquely identified we cannot rule out this possibility. It is likely that nests pair<sup>-1</sup> year<sup>-1</sup> will exhibit a negative association with  $S_n$ , however since the shape and magnitude of this interaction is unknown it has not been included in our analysis.

## Results

### *Nest survival and incubation behaviour*

On all but one of the nests where exclosures were used the adult birds rapidly accepted the structure and resumed incubation (time to resume incubation,  $\bar{x}$  = 11.45, S.E = 1.24

minutes n = 11 nests). On the one occasion where both adults did not accept the enclosure it was taken away after one hour and the nest was not included in the analyses. Nest survival was not affected by the presence of enclosures (Table 1;  $Z = 0.2132$ ,  $P = 0.5844$ ). Additionally, there was no difference in the likelihood of nest abandonment between the control and test group; one nest was abandoned in the treatment group and two in the control group. The majority of nest failure was attributable to predation. However, it was not possible to identify the relative importance of each nest predator species, or whether this differed from our previous work. Therefore it is not known for certain whether the enclosures reduced the effect of cats on nest survival and this was balanced by an increase from another species, or if there was no change at all.

**Table 1** - *Nest survival in St. Helena Plover showing daily survival and survival to hatching, the latter is calculated by raising daily survival rate to the power of incubation period, i.e. 30 days (Burns 2011, Chapter 6)*

<i>Group</i>	<i>Daily nest survival</i> ( $\pm 95\%$ CI)	<i>Survival to hatching</i> ( $\pm 95\%$ CI)
Control (n=11)	0.9532 (0.9441, 0.9623)	0.2375 (0.2254, 0.2503) <sup>a</sup>
Treatment (n=11)	0.9518 (0.9426, 0.9611)	0.2272 (0.2155, 0.2398) <sup>a</sup>

a: The 2.5 and 97.5 percentiles of distribution of 1000 estimates of survival to hatching, each one the product of 30 estimates of daily nest survival randomly chosen from the distribution of daily nest survival

Table 2 shows the full model and the minimal adequate model of total incubation time for the comparison between control and treatment groups. A quadratic relationship between time spent incubating and temperature was found; at low and high temperatures the nest was incubated for a greater amount of time than at intermediate temperatures. There was also a slight decline in total incubation time over the course of the experiment in both control and treatment groups. A similar analysis was completed solely for the treatment group nests, comparing incubation before and after the enclosure was put in place; the results qualitatively matched those presented here.

**Table 2** – Results of the logistic generalised linear mixed model of total incubation time (%), showing the full model and minimum adequate model. In all cases the random factor is nest ID,  $n = 62$ , no. of nests = 21, (one nest failed before observations could be undertaken). Df – Denominator degrees of freedom.

Fixed effects	Value	S.E	Df	t-value	P
<b>Full Model</b>					
Intercept	53.9729	23.4290	34	2.3037	0.0275*
Temperature <sup>2</sup>	0.07813	0.03888	34	2.009478	0.0525
Temperature	-3.9713	1.8866	34	-2.1050	0.0428*
Nest age at observation	-0.02884	0.1415	34	-0.2038	0.8397
Group : treatment	-0.3563	1.1278	19	-0.3159	0.7555
Day of Season	-0.04136	0.3054	34	-0.1354	0.8931
Temperature : day of season	-0.00058	0.01167	34	-0.04987	0.9605
Nest age : day of season	0.00095	0.003940	34	0.2408	0.8112
Nest age : group treatment	0.00233	0.08500	34	0.02745	0.9783
<b>Minimum model</b>					
Intercept	53.6015	21.6643	38	2.4742	0.0179*
Temperature <sup>2</sup>	0.07769	0.03405	38	2.2820	0.0282*
Temperature	-3.9698	1.7222	38	-2.3050	0.0267*
Day of season	-0.04155	0.01688	38	-2.4611	0.0185*

### *Nest predation and adult mortality*

#### Nest predation recorded on camera

The images from the camera deployed at a treatment nest show a cat eating the eggs. The video revealed that the cat gained access to the nest by entering directly through the wire mesh of the enclosure. The cat appeared to be struggling to get through the mesh, and took several minutes to gain entry. However, it managed to exit the enclosure on the opposite side quickly. The parent bird was not present in the video during this time. There were no visible signs that the enclosure had been damaged or tampered with in anyway; the mesh was not misshapen nor were there any signs of an attempt to uproot the enclosure or dig underneath it. This implies that the mesh size (5 x 10 cm) is simply too large to exclude all cats. It is thought that not all cats could get into the enclosures as one showed signs of attempted entry but the eggs were still present and the parents incubating. In this case the wire mesh was slightly misshapen but the enclosure was still firmly fixed into the ground, indicating that increasing the gauge of the wire might

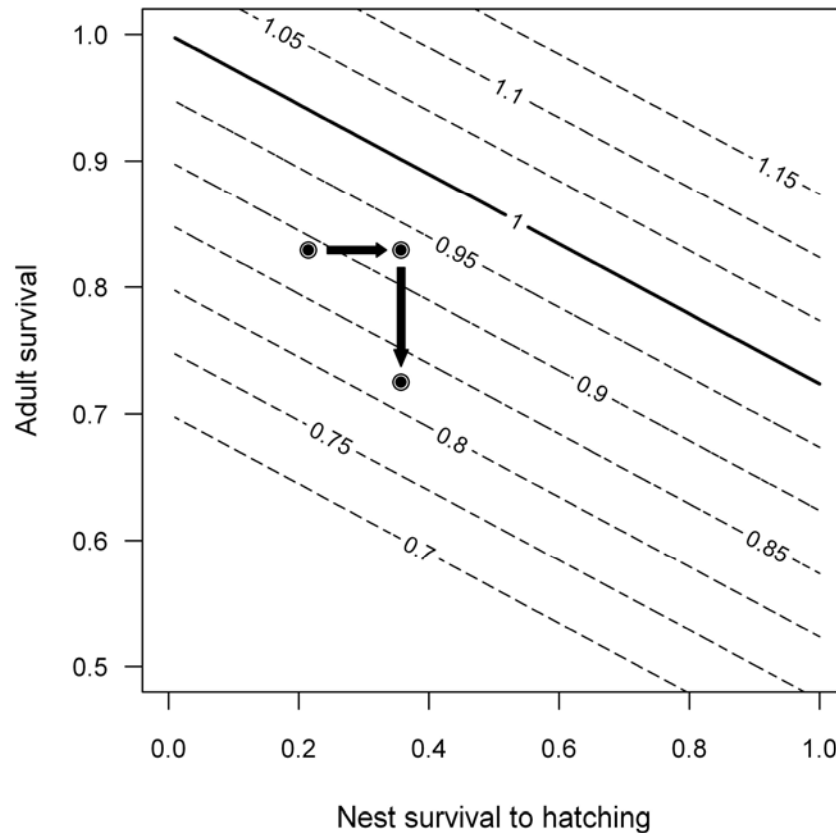
have been useful. If exclosures are excluding some cats then their use may then still be of some benefit to nest survival but it is likely that a far larger sample size would have been required in order to detect this.

#### Adult predation

In the final week of the trial the remains of two adult birds were found near the nest, each associated with an exclosure. The nest camera had been set up at one of the nests where adult mortality occurred. Although this camera did not capture the attack on the adult, the footage does show a cat eating the eggs on the evening of the adult mortality, strongly suggesting that a cat was responsible for the adult deaths. The two nests where adult predation occurred were around 800 m apart and so could be within the home range of a single cat, but we cannot know if an individual had learnt to associate the exclosures with the presence of eggs and birds and was responsible for both deaths. However, neither from the video evidence, nor any other evidence, is it clear how the cat managed to catch the two adult birds. Most feathers were found within a meter of the exclosures, but not inside, indicating that the birds were caught as they were leaving or returning to the nest, possibly as they were going through the mesh. Predation upon adult birds appears to be very rare and evidence of it has only ever been found on one or two occasions (McCulloch 2009), none of them during the three field seasons that one of us (FB) has recently completed.

#### *Modelling the impact of nest exclosures*

Using existing estimates of demographic parameters the St. Helena Plover population is predicted to decrease (Figure 3). Given the observed rates of brood and juvenile survival, the potential increase in nest survival from the use of exclosures would be insufficient to reverse this decline, even though it would have the effect of raising the population growth rate. From Fig. 3 we can see that the decrease in adult survival observed in this study is likely to more than negate the potential increase in nest survival resulting from the use of exclosures.



**Figure 3** – *Impact of nest exclosures on St. Helena Plover. Solid line: conditions required to give a stable population size calculated using observed population averages for juvenile and brood survival. Dashed lines: the same relationship but for the indicated population growth rates. The points show the three scenarios described in the methods section, following the order of the arrows: i) Baseline of observed  $S_A$  and  $S_n$ ; ii) The potential increase in  $S_n$  from exclosure use, assuming  $S_A$  remains unchanged; iii) Both the potential increase in  $S_n$  and the concurrent observed decrease in  $S_A$ .*

## Discussion

Smith et al.'s (2011) meta-analysis found an overall trend towards increased nest survival from nest exclosure use. Their analysis compared eight long term studies of nest exclosures for ground nesting birds; seven of which were on North American *Charadrius* species and one on ducks. Contrary to their finding our study found no difference in nest survival between the study groups. This is likely to be because the exclosures did not exclude all cats, and the use of exclosures probably made nests easier for cats to locate. As 5 x 10 cm mesh is the most common type used for exclosures this

finding is of relevance to conservation managers and decision makers, in particular those working in localities where cats have been recorded as a major nest predator (Dowding and Murphy 2001; Moore 2005). Some exclosures studies for Piping Plover *Charadrius melodus* (Deblinger et al. 1992; Mabee and Estelle 2000; Richardson 1999; Rimmer and Deblinger 1990), and Snowy Plover *Charadrius alexandrinus* (Mabee and Estelle 2000) have used 5 x 5 cm mesh, which is the next smallest mesh size commercially available and would hopefully exclude even small cats. However, although St. Helena Plovers are similar in body size to these species they are significantly taller due to their long legs (tarsus 40.7 mm, compared to 19.4 and 27.5 for piping and snowy respectively (FB Unpublished data, Cohen 2005; Lislevand et al. 2007)). Therefore it is not clear whether the plovers would enter such an exclosure, and if they did whether such a mesh size would impede their exit. Alternatively a custom made exclosure could be designed, perhaps having a mesh width of 4 cm; however this would substantially increase project costs.

A unique aspect of our study was our investigation of the impact of exclosures on the incubation behaviour of parent birds. The average total incubation time (92%) was similar to that found for other similar species (Baudains and Lloyd 2007; Kosztolányi and Székely 2002a; St Clair et al. 2010a), although nest observation methods were not identical in each study. It is reassuring for those using exclosures as a management technique that no difference was found in total incubation time between groups or, within the treatment group, before or after application of the exclosure. This indicates that the parent birds behave as normal when incubating inside an exclosure. There could, however, be more subtle influences that were not detected in our study. For example, there could be changes in the balance of incubation between the parents. Additionally, we only monitored diurnal incubation behaviour so there may be undetected changes in the nocturnal sex-specific time-budgeting. Neihaus (2004) reported a reduction in total incubation time, but this was due to constant harassment by predators rather than the exclosure per se.

**Table 3** – Summary of adult mortality associated with nest exclosures in shorebirds

<i>Species</i>	<i>Adult Mortality</i> <sup>a</sup>		<i>Daily Nest Survival</i> <sup>b</sup>		<i>Predator</i>	<i>Study</i>
	Treatment	Control	Treatment	Control		
Killdeer <i>Charadrius vociferus</i>	3.85 (104)	0 (106)	0.97	0.92	Long-tailed weasel <i>Mustela frenata</i>	(Johnson and Oring 2002)
	8.33 (24)	0 (34)	0.963	0.951 <sup>c, d</sup>	Mink <i>Mustela vison</i>	(Nol and Brooks 1982)
Pectoral Sandpiper <i>Calidris melanotos</i>	3.33 (30)	0 (214)	0.99	0.96	Arctic fox <i>Alopex lagopus</i>	(Niehaus et al. 2004)
Piping Plover	2.69 (2710)	0 (840)			Raptor	(Murphy et al. 2003b)
	1.56 (64)	0 (72)	0.985	0.956		(Richardson 1999)
Redshank <i>Tringa totanus</i>	12.16 (74)	1.61 (62)	0.997	0.964		(Isaksson et al. 2007)
	2.82 (666)	0.860 (698)			Raptor	(Neuman et al. 2004)
Snowy Plover	2.92 (274)	0 (192)				(Hardy and Colwell 2008)
St. Helena Plover	8.33 (24)	0 (24)	0.953	0.952 <sup>c</sup>	Cat	this study

a: Percent mortality of parent birds (number of parent birds)

b: Mayfield method. Nest Survival is shown if reported in the study and not subject to experimental bias.

c: Non significant differences in nest survival, tests of significance taken as published and not re-analysed

d: Daily nest survival not presented in paper so calculated from data presented



There are a growing number of examples which show an increase in adult mortality associated with the use of nest exclosures (Table 3). In contrast no increase in adult mortality has been reported for dunlin *Calidris alpina* (Pauliny et al. 2008) and northern lapwing (Isaksson et al. 2007). Few generalisations can be drawn from Table 3, which shows cases distributed across a wide range of prey and predator species. Additionally, cases are reported that use various exclosure designs, and were undertaken in various habitats and geographical locations. Some suggestions have been made in the literature of characteristics that mediate the risk of adult mortality; however these are necessarily post hoc, as researchers are reluctant to continue with the use of a method that is thought to suppress the adult survival. Murphy et al. (2003b) suggested that adult mortality was lower in treeless environments due to lower densities of raptors; the dominant predator of adults in their study. Murphy's study also suggested that adult mortality was lower at nests protected by larger exclosures. However, an increase in adult mortality has been found at all commonly used types of exclosure design, regardless of their size or shape. Isaksson et al. (2007) suggested that redshank were at greater risk of mortality at the exclosure compared to northern lapwing, where no adult mortality was observed, due to their late flushing behaviour. Nevertheless there appears to be no clear risk factors that can be generalised across all cases and therefore management prescriptions will have to be condition dependent. Although it is not fully understood why birds incubating inside nest exclosures are more vulnerable to predation, one criticism of nest exclosures is that they make normally cryptic nests obvious in the landscape if a predator can learn to associate the exclosures with nests. An increase in visibility of nests with exclosures accompanied by predator learning could mean that predators can get closer to nests before the adult birds are aware of them. In this situation cats would be able to detect the presence of a nest from a greater distance and approach cautiously, therefore getting closer to the nest before being seen by the parent bird. We can detect predator learning when predation of adults occurs in episodes where several exclosures were targeted in the same area at once. This was the case in the current study and in Hardy & Colwell (2008), Murphy et al. (2003b) and Neuman et al. (2004). The use of dummy exclosures could potentially disrupt this association. However, their effectiveness may be limited if there is little cost to the predator in checking an empty exclosure. It has also been postulated that parent birds feel safer inside the exclosures and respond less to potential predators outside the exclosure (Gulickx and Kemp 2007), although Richardson (1999) found no difference

in flushing distance between enclosed and control nests. If protected nests in general survive for longer than control ones, and if the threat of adult mortality is a constant daily risk then it is possible that some of the observed increase in adult mortality at enclosed nests can be explained simply by the greater exposure time they experience. However, since several studies with large sample size have observed no mortalities associated with control nests it is unlikely that exposure time alone explains the increase in adult mortality. The estimated increase in adult mortality may be biased if nests are not randomly allocated into control and treatment groups, for example if exclosures were used only in areas of high predator density. Of the studies listed in Table 3, three did not allocate exclosures randomly, as they were reporting on unexpected consequences of routine management, rather than a controlled experiment. Nevertheless, a sufficient number of well designed studies are available to convince us that this increase in adult mortality is not an artefact of study design.

Our results indicate that even a modest decrease in adult survival could substantially reduce the overall positive effect of nest exclosures on the population (Fig. 3). It is difficult to extrapolate our results shown in Fig. 3 to other species because not all the necessary demographic parameters are known. Nevertheless, it is likely that there would at least be a substantial reduction in effect size in each case. This decrease in effect size may mean that targets to stabilise or increase the study population are not met, or that nest exclosures cease to be the most cost effective conservation technique. Few studies have investigated the population-level or long term effects of nest exclosures on populations (Murphy et al. 2003b; Neuman et al. 2004) and therefore for the majority of cases the impact of decreased adult survival may be overlooked. Although our estimate of the decrease in adult survival is uncertain as it was extrapolated from a small sample size, it is likely to be conservative as it does not take into consideration indirect negative effects, such as the time taken for the mate of the predated adult to find a new partner, changes in the behaviour of survivors towards predators, or the ethical concerns about the use of a technique that leads to increased adult mortality. Additionally, there is some suggestion that the elevated incidence of nest abandonment observed in some studies could be due to unrecorded adult mortality (Murphy et al. 2003b). A final consideration is the relationship between nest survival and the number of nests a pair has in a season. Although not modelled here, this relationship is likely to moderate the benefit of nest exclosures, in particular in species

where there is a constrained breeding season or for those that do not double brood. Therefore, the real effect of nest exclosures can only be seen by comparing estimates of seasonal productivity. Several studies have already sought to do this (Larson et al. 2002; Murphy et al. 2003a; Neuman et al. 2004; Pauliny et al. 2008), and some have found that the observed increase in nest survival is not translated into an increase in productivity (Neuman et al. 2004; Pauliny et al. 2008).

### *Management Implications*

It is clear that nest exclosures using 5 x 10 cm mesh are not suitable in an area where nest predation is dominated by cats, especially where these are typically of small stature or under-weight. Additionally, circumstantial evidence suggests that cats can learn to associate the presence of exclosures with that of nests leading to a decrease in adult survival. This decrease, given observed values of other demographic parameters, would totally negate the projected increase in nest survival even if exclosures prevented nest predation by cats. Therefore, even if a different design of exclosure were to be used there would be little or no benefit to the population. Thus, even though St. Helena Plovers readily accept nest exclosures and their incubation does not appear to be affected, further use of exclosures is not recommended for this species. More generally, there is a need for more studies that look into the overall effects of the use of nest exclosures on target populations, taking into consideration annual productivity and adult survival in particular, as doing so would allow managers to prescribe circumstances under which it would be beneficial to use nest exclosures for a given species or population.

### **Acknowledgements**

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**Appendix 1** - *Estimates of Demographic Parameters used to create Figure 3. Adult, juvenile and nest survival were estimated using programme MARK, brood survival is a Mayfield estimate.*

<i>Parameter</i>	<i>Estimate (95% CI)</i>
S <sub>J</sub>	0.4710 (0.4234, 0.5132)
S <sub>A</sub>	0.8292 (0.8071, 0.8466)
S <sub>N</sub>	0.2148 (0.2026, 0.2243)
Brood survival (S <sub>B</sub> )	0.3478 (0.3256, 0.3702)
Chicks successful brood <sup>-1</sup> (C <sub>B</sub> )	1.36
Nests pair <sup>-1</sup> year <sup>-1</sup> (N <sub>P</sub> )	2.4812

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## **Chapter 6: Persistence of an island endemic in a heavily altered environment: assessing outcomes of conservation management options**

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## Abstract

Insular species have suffered dramatically from habitat change and introduced species following colonisation by humans of the world's islands. Many species remain threatened; one of these is the St. Helena Plover *Charadrius sanctaehelena*, endemic to the isolated island of St Helena in the Atlantic Ocean and currently classified as critically endangered. Although recent work has begun to understand the population ecology of this species the actions required to secure population recovery remain unclear. An individual stochastic metapopulation model was therefore developed in order to assess how variation in demography and life history parameters affects the population growth rate, and to compare the outcomes of development and conservation management options. The model was parameterised using empirical estimates of the demography and life history of the St. Helena Plover. Using the probability distribution of current estimates of demographic parameters the global population of this species was predicted to be declining slowly,  $r = -0.034$ . The rules governing natal dispersal influenced overall growth rate variably under different management scenarios. Refinement of these with additional data would improve the predictive ability of the model. The model has three specific predictions. First, one site, Deadwood Plain, was found to be of key importance to the metapopulation. It is a source of juvenile birds that support other sites where productivity is lower, its removal from the model led to a reduced population growth rate and control of nest predators had the largest beneficial effect to the metapopulation if carried out here. Second, targeting conservation management towards areas with lower adult survival is likely to be advantageous to the population, as this parameter had the greater influence on population growth rate in sensitivity analysis. Third, the benefit of reducing densities of nest predators was greater than the benefit of increasing the area of breeding habitat, in particular in areas of low productivity. However, the benefit of habitat improvement increased when predator control was conducted simultaneously. We conclude that the metapopulation model produced specific insights into demography of St. Helena Plover and offered a tool to assess various management options, future works are needed to test the efficacy of these predictions.

## Introduction

Birds endemic to isolated islands can be characterised by certain attributes compared to their mainland relatives, for example; body size change; loss of dispersal ability or loss of defensive adaptations (Clegg and Owens 2002; Whittaker and Fernández-Palacios 2007; Williamson 1981). These adaptations have culminated in the loss of powered flight in many island forms (Medeiros and Gillespie; Slikas et al. 2002). The combination of these attributes left insular forms vulnerable to the dramatic environmental changes that followed the discovery of their homelands by humans. Species restricted to islands make up around 17 % of all bird species, however, more than 80 % of bird extinctions since 1600 were of insular forms (Johnson and Stattersfield 1990), and many more species remain threatened.

Demographic models have been increasingly used to try to understand the population dynamics and risk of extinction faced by rare and threatened species over the past twenty years (Beissinger and McCullough 2002). The utility of demographic models to advise conservation management is most famously described by the case of the Loggerhead turtles *Caretta caretta*. In their landmark paper Crouse et al. (1987), using the matrix approach to population modelling, showed that turtle populations would benefit more from conservation targeted at increasing adult survival; whereas previous management had been focused on nest protection. More recently individual based demographic models have been developed. Although not unique to this modelling approach, these computer simulations are characterised by the inclusion of several types of stochasticity. For instance, the survival and productivity of individuals is described by the probability distribution of the empirical estimates, therefore incorporating demographic stochasticity. The individual approach also facilitates incorporation of parameters such as the social structure of the species concerned, or variation in the sex ratio or mate availability (Lacy 2000). Generic software for creating individual population models is freely available, for example Vortex (Lacy et al. 2005). Vortex is extensively used by conservation practitioners and scientists worldwide. For example Fessl et al. (2010) used Vortex to compare the population responses of the rarest of Darwin's Finches to different predator control options. Additionally, several authors have developed custom built individual based population models to address a specific system or species. For instance Ratcliffe (2005) presented a re-nesting model that was

used to understand the optimal land management for Black-tailed Godwits *Limosa limosa* in relation to flood risk. Such models have also been used to understand the population consequences for Great Blue Herons *Ardea herodias* of chronic exposure to chemical contaminants (Matsinos and Wolff 2003), and to investigate the influence of environmental change on the mortality of non-breeding shorebirds (Stillman and Goss-Custard 2010). One key benefit of a custom built model is flexibility, allowing any novel aspect of the target species' biology or ecology to be included, as well as variation in these parameters based on an individual's current condition or past experience. Researchers can also dictate the output of the model and therefore investigate trends in whatever parameter they wish. Finally, it is often easier to understand the constraints, assumptions and mechanisms used in a custom model.

Despite, or perhaps because of, their extensive use, there has been much debate about the ability of demographic models to give robust conservation advice (Beissinger and Westphal 1998; Coulson et al. 2001b). The key outcome of this debate has been a keener appreciation of what can reasonably be inferred from these models and the situations where they are informative (Beissinger and McCullough 2002; Reed et al. 2002).

In this paper we set out to develop an individual based metapopulation model for the endangered St. Helena Plover *Charadrius sanctaehelenae* (also known as the Wirebird), endemic to the isolated Atlantic island of St Helena. The birds of St Helena Island conform to the general pattern of island life. There were at least six endemic species of bird present when the island was discovered in 1502 and since this time all but the plover have become extinct (Ashmole and Ashmole 2000). It is likely that the St. Helena Plover was the only one of the endemic land birds that retained substantial powers of flight (Olson 1975), helping it to survive in the altered landscape. Regardless of its survival to date, the persistence of the St. Helena Plover is not assured. The species is currently classified as Critically Endangered due to a dramatic decline in the population in the early years of this decade (BirdLife International 2009; McCulloch 2009). Although numbers appear to have stabilized in the intervening years the global population size is very small ( $\bar{x}$  (2007 – 2011) = 352.8, SD = 32.7) (SHNT 2011), and the key parameters influencing its population dynamics remain unknown.

Population modelling was made possible by recent research, which has for the first time investigated St. Helena Plover demography and started to investigate how this interacts with the environment (Burns 2011, Chapters 2 - 4). Our model was used to compare the predicted outcomes of potential management scenarios and to investigate the influence of model components at the population level, both of which are suggested to be legitimate uses of such models (Coulson et al. 2001b). One of the key weakness of demographic models, in particular those that include spatial heterogeneity, is the volume of data required to parameterise them (Beissinger and McCullough 2002). In our case, although we do not have a long time series of data, the life history of St. Helena Plovers and the relative simplicity of the ecosystem they inhabit make obtaining the necessary data a more realistic task. The St. Helena Plover forms a single metapopulation, it is non-migratory, and it has a small population size and the smallest global range of any wader (McCulloch and Norris 2001). A considerable fraction of the population can therefore be studied throughout all life stages. Data collection is further assisted as, in common with many island species, the St. Helena Plover is relatively tolerant of humans.

The following questions were investigated using the population model:

1. What is the best estimate of current population growth rate and how is this affected by varying input demographic parameters and other life history variables?
2. How do different decision-making rules for natal dispersal influence population growth rate?
3. What would be the repercussions of the removal, for example due to development, of one of the key plover breeding sites, and could the creation of additional habitat elsewhere compensate for this?
4. What are the relative benefits of two conservation management strategies, reducing nest predator densities or increasing the area of suitable breeding habitat?

## **Methods**

### *Data collection*

The St. Helena Plover is endemic to St Helena (15°58'S 5°43'W), a UK Overseas Territory. The island has changed dramatically since its discovery in 1502. Although no mammals are native to the island, many invasive mammal species are now present,

including cats *Felis catus*, dogs *Canis lupus familiaris*, Brown rats *Rattus rattus*, Norwegian rats *R. norvegicus*, mice *Mus musculus*, as well as an invasive bird, the Common Myna *Acridotheres tristis* (Ashmole and Ashmole 2000). The landscape of St Helena is also much changed since pre-human times and plovers now use grazing pasture as well as more natural semi-desert habitat. Field data used to estimate model parameters were collected between October 2007 and March 2008 and between October 2008 and October 2009. Five study sites were used, encompassing roughly half of the global population. These are named, Deadwood Plain (DWP), Broad Bottom (BB), Man and Horse (MH), Upper Prosperous Bay (UPB) and Prosperous Bay Plain (PBP). The first three sites are pasture and the latter two semi-desert. Few birds were observed at Prosperous Bay Plain, and as the two semi-desert sites are contiguous, data from them were pooled and referred to as Prosperous Bay (PB). Full details of the methods used have been given elsewhere (Burns 2011, Chapters 1 - 5), and follow the guidance set out in Szekely (2007). In order to estimate annual productivity a subset of colour ringed pairs were followed for a 12 month period, (Oct 08 to Oct 09) locating and monitoring all breeding attempts.

### *Model Description*

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al. 2006). The model code is shown in Appendix 1 and was written using Visual Basic 2008 (Microsoft 2008).

**a) Purpose:** The purpose of the population viability model is to investigate how the population dynamics of the St. Helena Plover are influenced by variation in demographic and other life history parameters and also by metapopulation structure. Simulations will attempt to mimic alternative conservation or development options and therefore allow the influence of these on the population to be estimated and compared.

**b) Entities, state variables, and scales:** The agents in the model are individuals, territories and sites. Individuals have state variables of stage (juveniles, adult). Juveniles have the state variables of age (days) and site membership. There are no age specific parameters once adulthood has been reached. Adults have state variables of status (territorial, non-territorial), and site membership and, if territorial, have an

additional variable of territory membership. Territories have the state variables of identity, status (empty, occupied (two birds), breeding (one or two birds)) and site membership. There are four sites in the model that mimic the four study areas described above. Sites have associated demographic estimates of nest survival, brood survival, juvenile survival and adult survival. Sites also have state variables of initial number of occupied territories and hence individuals, and total number of territories (carrying capacity). Territories are uniquely identified rather than individuals and individuals do not retain state variables upon leaving a territory. Territories within a site are all assumed to be of equal quality. The temporal scale of the model is daily, and data were extracted annually. Spatial scale is four sites with dispersal at the juvenile stage.

**c) Process overview and scheduling:** For each set of starting conditions the model is run for 50 years and 100 replications unless otherwise stated. Each day the model carries out the sub-models described in section (g) for each site in turn (Table 1; Figure 1). Each sub-model is performed by agents in numerical order.

**d) Design concepts:**

Emergence - The dynamics of the population as a whole and at the site level are emergent properties of the model.

Adaptation and Objectives - Some dispersal rules allow juveniles to recruit into a high quality site in order to maximize chance of finding a mate and therefore fitness.

Sensing - Depending upon the simulation, juvenile individuals are assumed to be able to sense when a site is full, or assess site quality.

Stochasticity - Demographic stochasticity is modelled by comparing randomly generated probabilities to average parameter estimates for all demographic and behavioural parameters. Environmental stochasticity is included by selecting new demographic estimates each year from the cumulative normal distribution. No spatial or temporal autocorrelation was included, nor covariance between vital rates.

Catastrophes were not included as the environment on St Helena is not subject to intense weather events. No individual stochasticity was included in the model.

**Table 1– Outline of structure of the population model**

<i>Process</i>	<i>Pseudo-code description</i>
Initiation	Set up starting conditions Return to starting conditions after one model replication
Mortality of floating birds	Die with probability according to adult mortality
Fill territories	Do for each empty territory - Floating individuals move into empty territory based on the chance of there being a male and a female in the floating group - Update array summarizing the number of territories of each status
Initiate breeding	For each occupied territory - Initiate nesting attempts with probability according to $p_n$ - If nest initiates determine clutch size, laying period and nesting period
Breeding	For each breeding territory - End breeding attempt with probability according to nest mortality and brood mortality - Reduce time to hatching or fledging by one day - Hatch nest or fledge brood if time to hatching or fledging is zero - If hatch determine brood size at hatching - If fledge determine brood size at fledging and transfer fledglings into juvenile group
Territorial adult mortality	For each adult in each territory - Die with probability according to adult mortality - Only birds left single with chicks remain on territory, those nesting or not breeding return to the floating population <b>This command runs at the start of the Initiate Breeding and Breeding sub-models prior to other tasks</b>
Juvenile mortality	For each juvenile - Die with probability according to juvenile mortality - Age by one day
Recruitment	For each juvenile - Recruit into the floating population with a probability according to observed mean age at recruitment and its standard deviation - Disperse between sites according to simulation specific rules
Update	The array summarizing the number of territories of each status is updated

Observation - The model begins in the middle of austral winter, Julian day 183, as this is the point at which there is the least breeding activity and therefore the starting conditions are easier to simulate. Starting conditions are saved to file at the beginning of each simulation and then at then a summary is taken at the end of each model year, at Julian day 182. The year, replication and simulation number are stored, as are that year's demographic estimates. The number of territories of each status and the number of birds in the floating and juvenile groups are recorded, along with the total number of nests, broods, chicks, successful broods, fledglings, recruiters and adults dying that year. Much of the information saved at the point of summary is used for model verification. The most important parameter for further analysis is the total number of adults at a site, which can be used to estimate the magnitude of, and variation in, the population growth rate over model replicates at the level of each population and the metapopulation.

**e) Initialisation:** Table 2 shows the starting values for each input parameter and if appropriate the associated standard error.

**f) Input data:** The model does not use input data to represent time-varying processes

**g) Sub-models:**

Fill Territories – Territories are filled by estimating the chance that there is both a male and a female amongst the floating population for that site. If a pair move into a territory and there are still more birds in the floating population the procedure is repeated.

Initiate Breeding – St. Helena Plovers breed throughout the year, although there is a seasonal cycle of breeding propensity. In order to estimate the chance of nest initiation throughout the year 32 pairs of birds were monitored for a year and the initiation date of all breeding attempts recorded. The total number of attempts initiated each week was used as the response variable in a Glm with Poisson errors. The best fit to the data was chosen using AIC (Akaike's information criterion), giving the minimum adequate model:

$$\ln(P_n) = 1.68 - 0.196w + 0.00367w^2 ; w = \text{week of year}$$



The daily probability of nest initiation pair<sup>-1</sup> was calculated using Equation 1. The chance of nest initiation is corrected in the model given the number of pairs available to start nesting that day out of the total occupied territories.

$$1 - \left( \frac{32 - e^{p_n}}{32} \right)^{\frac{1}{7}} ; \text{Equation 1}$$

Although our best effort was made to find all the nests inevitably some were missed as they failed before discovery. As the number of nests pair<sup>-1</sup> year<sup>-1</sup> is likely to strongly influence population dynamics we attempted to estimate the proportion of nests missed and use this as a correction factor in the model; denoted Nest detection correction factor in Table 2. This calculation was done on a site specific basis as it will interact with nest survival, which varies between sites. Two calculations were conducted, the proportion of nests that survived for such a short period of time that they were not present during any study visit ( $p_1$ ), and the proportion of nests that were present on at least one study visit but were missed due to a detection probability of less than one ( $p_2$ ). A simulation was run to generate 10000 estimates of incubation duration for different levels of daily nest survival. From this the proportion of nests not present during any visits could be calculated:

$$p_1 = \left( \sum_{i=0}^t \frac{a_i(t-i)}{t} \right) / 10000$$

where  $t$  is the average time between site visits, and  $a_i$  is the number of failed nests of age  $i$  (days). The simulation was also used to calculate the average duration of incubation, conditional on the nest being present during at least one site visit ( $I$ ).

Average detection ( $\bar{d}$ ), was calculated:

$$\bar{d} = \left( \sum_{v=1}^3 \frac{f_v}{n_v} \right) / 3 ; p_2 = (1 - \bar{d})^{(I/t)}$$

where  $f_v$  is the number of nests found on visit  $v$ , and  $n_v$  is the number of nests available to be found on visit  $v$ ; those initiated between visit  $v - i$  and visit  $v$  plus those not found on previous visits.  $p_2$  was found by raising the reciprocal of  $\bar{d}$  to the power of the average number of visits a nest survived for given current daily nest survival ( $I / t$ ). The total proportion of nests missed is the sum of  $p_1 + p_2$ .

**Table 2** – *Model starting conditions*

<i>Parameter</i>	<i>Refers to</i>	<i>Initial Value</i>	<i>SE</i>
Daily nest survival (Beta model coefficients) <sup>1</sup>	DWP	0.9738 (4.2007)	(0.3397)
	BB	0.9574 (-0.4838)	
	MH	0.9181 (-1.3582)	
	PB	0.9376 (-0.8955)	
	Age of nest <sup>2*</sup>	(0.008903)	
	Season day*	(-0.01148)	
Daily brood survival <sup>3</sup>	All	0.9711	0.005291
Daily adult survival (Beta model coefficients) <sup>4</sup>	DWP, BB, PB	0.9997 (1.7771)	(0.04)
	MH	0.9990 (1.2291)	
Daily juvenile survival <sup>4</sup>	DWP	0.9985	0.0006
	BB, MH, PB	0.9971	
Mean age at recruitment – days	All	329.17	62.454
Carrying capacity (Initial occupied territories) <sup>5</sup>	DWP	124 (80)	
	BB	44 (26)	
	MH	44 (38)	
	PB	52 (48)	
Floating*	All	Empty	
Juveniles <sup>6*</sup>	DWP	28	
	BB	6	
	MH	4	
	PB	10	
Nest detection correction factor, see text for details*	DWP	1.3220	
	BB	1.1666	
	MH	1.3836	
	PB	1.3227	
Incubation period <sup>7</sup>		28	
Laying period*		1 day per egg	
Fledging period <sup>7</sup>		36	
Clutch size	1	0.1118	
	2	0.8882	
Addling & partial predation		0.15	
Average brood size at fledging – for 2 chick brood		1.5	

1: Data from Burns 2011 Chapter 2; 2: \* = fixed parameter in model; 3: Mayfield estimate

4: Calculated from back-transformed monthly survival rates, data from Burns 2011 Chapter 4

- 5: Census data courtesy of St Helena National Trust. The four study sites encompass half of the population and therefore numbers have been doubled to represent the whole population.
- 6: Number of juveniles predicted to be present mid-winter given productivity of each site and number of pairs present.
- 7: Supplementary data from Neil McCulloch

The derivation of nest survival estimates is described elsewhere (Burns 2011, Chapter 2). Nest survival was calculated using data from the core breeding season only because too few nesting attempts are made during the winter to make any meaningful conclusions about cyclic seasonal effects. Therefore during the individual based modelling winter nest survival is estimated using an average value for day of season. Brood survival was based on the Mayfield estimator (Mayfield 1975). Sample size precluded site specific differences being investigated. As no difference between the two habitat types was found, a single value was used across all sites. The breeding sub-model follows breeding attempts through nesting and brood stages; each day testing whether an attempt survives, ends successfully or fails. If a mated adult dies during the nesting phase of a breeding attempt, the attempt fails and the remaining adult returns to the floating population. If a mated adult dies during the brood phase then the attempt continues but the survival probability is reduced by half.

Territorial Adult Mortality - Juvenile and adult survival were estimated using programme MARK (Burns 2011, Chapter 4).

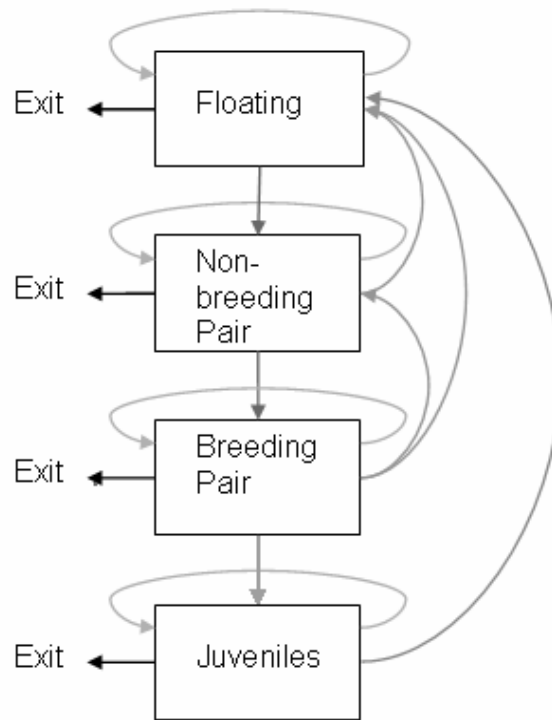
Recruitment - Juveniles were eligible to recruit into the adult population at 204 days old. Recruitment probability is determined by the normal distribution of observed recruitment ages. If juveniles reach 455 days old they recruit automatically. Natal dispersal occurs at the point of recruitment; the simulations section below shows the different modes of dispersal tested. Breeding birds have only been observed moving to a new territory in a different site three times out of 104 adults ringed; 73 of which were re-sighted at least a year after ringing (Burns 2011, Chapter 4), and therefore no dispersal in adulthood is included in the model.

Update - At the end of each site day the number of territories in each state is recalculated. On Julian day 183 yearly summary parameters are reset and all parameters are reset at the beginning of a new replication.

**h) Verification and Simulation experiments:** All analyses were conducted using Programme R (R Core Development Team 2004). To test if the demographic parameters were being re-estimated correctly the output mean was compared to the

starting value and histograms were inspected for deviations from normality. Although the presence of stochasticity in the model led to variation in model output, because the models were replicated many times the average output should closely resemble the input. Outputs for all demographic parameters were checked in this way.

1. Baseline population growth rate and Sensitivity – For all models in this section 100 sets of input values were used, and each set was repeated 50 times unless otherwise stated. The baseline population growth rate was estimated using sets of input values chosen from a cumulative normal distribution of each estimate. For each set the intrinsic population growth rate ( $r$ ) was calculated, resulting in a distribution of growth rates. Ideally in order to understand the influence of each model parameter and its interactions on population dynamics all parameters would be altered simultaneously.



**Figure 1** – *Simplified structure of the population model, showing the possible transitions each day*

Given available computing power, however, sensitivity testing was undertaken in two parts. Firstly, the influence of the four demographic parameters was investigated. For simplicity all population specific estimates of a particular demographic rate were varied by the same amount. This was accomplished by adding a randomly generated correction factor, selected from a uniform distribution with the standard error of the estimate but a mean of zero. Demographic parameters were altered simultaneously in order to incorporate interactions. During demographic analysis the carrying capacity of each site was increased in order to observe the influence of variation in vital rates more clearly. Secondly, the influence of varying life history parameters: incubation duration, fledging duration, fledglings per successful brood, nests pair<sup>-1</sup> year<sup>-1</sup>, was investigated to understand how sampling error in these parameters affects model output, termed error sensitivity. Parameter values were randomly selected from their uniform distributions. For both sensitivity datasets the population growth rate for each set of starting conditions was calculated, and linear modelling was used to determine the relative importance of each parameter. Finally, the influence of the starting population size was investigated by running the model with starting population sizes ranging from half to twice that of current values. All populations were altered synchronously and each set of starting conditions was repeated 100 times.

2. Dispersal - The true mode of natal dispersal within the population is not known. Field data indicates that both sexes do disperse and that at least in one study site around 30% of birds disperse and 70% remain in the natal area (FB, unpublished data). The purpose of this simulation was to understand the importance of dispersal on population dynamics by comparing different dispersal rules. Six options for dispersal were tested: 1: no dispersal, 2: dispersal only when natal site is full, 3: random dispersal, 4: dispersal probability inversely correlated with distance from natal site, 5: dispersal probability directly correlated with an index of site quality based on productivity, 6: dispersal probability directly correlated with the number of available territories. For all options other than no dispersal a bird did not disperse to a full site unless all sites were full. Since the true mode of dispersal is not known all the other simulations described here use the three most likely options, 4-6 (for justification see results). For this and all subsequent simulations population growth rate was estimated for each model replication.

3. Site removal - In the future there is a real threat of development on one or more St. Helena Plover breeding sites, which could reduce the suitable area of habitat or

completely remove it. Here we investigate the impact of site removal on population dynamics. One site at a time was removed and the adult birds had to find a new territory elsewhere; the patterns of dispersal were as those normally used for juveniles. No additional risk of mortality due to displacement was included. A further set of simulations added an extra 0.5 km<sup>2</sup> of habitat to remaining sites as well as removing one site. In reality half of each site was removed at a time as each site in the Visual Basic (VB) model is equivalent to twice the population size of our actual study sites.

4. Conservation Management options - Previous research has shown that the density of predators at a site greatly influences nest survival and is also likely to alter brood survival (Burns 2011, Chapter 2). Although several nest predators have been identified, predation by cats has been found to largely determine nest survival; therefore simulations were run investigating the effect of reducing cat predation. Firstly, cat predation on nests was reduced by 0.25 and 0.5 at each site in turn. Although difficult to assess due to precocial nature of the plovers, it is likely that predation is the dominant cause of failure at the chick stage and that cats are the dominant predator species. For this simulation it was estimated that cat predation accounted for half of brood failure. Daily brood failure was reduced by 0.125 and 0.25 to reflect this. The number of chicks fledged brood<sup>-1</sup> was also increased accordingly. The possibility that reducing cat density would increase adult or juvenile survival was not investigated here and it was assumed that there was no numerical response in the population size of any other species as a result of reducing cat numbers.

Previous research has indicated that habitat improvement acts primarily to increase carrying capacity rather than alter demographic rates (Burns 2011, Chapter 3). It has also been shown that large areas of each study site are currently in sub-optimal condition and do not support plover territories. A second set of simulations investigated the outcome of undertaking predator control and/or habitat improvement at an island-wide level. For the latter, carrying capacity was increased at each site to mimic the improvement of 0.5 km<sup>2</sup> but demographic rates remained unchanged. In the VB model the effect sizes described here were halved, as each site in the VB model represented twice the population size of the actual study sites. Therefore, in this and the previous simulation the results represent modification of actual sites, not the artificially large sites in the VB model.

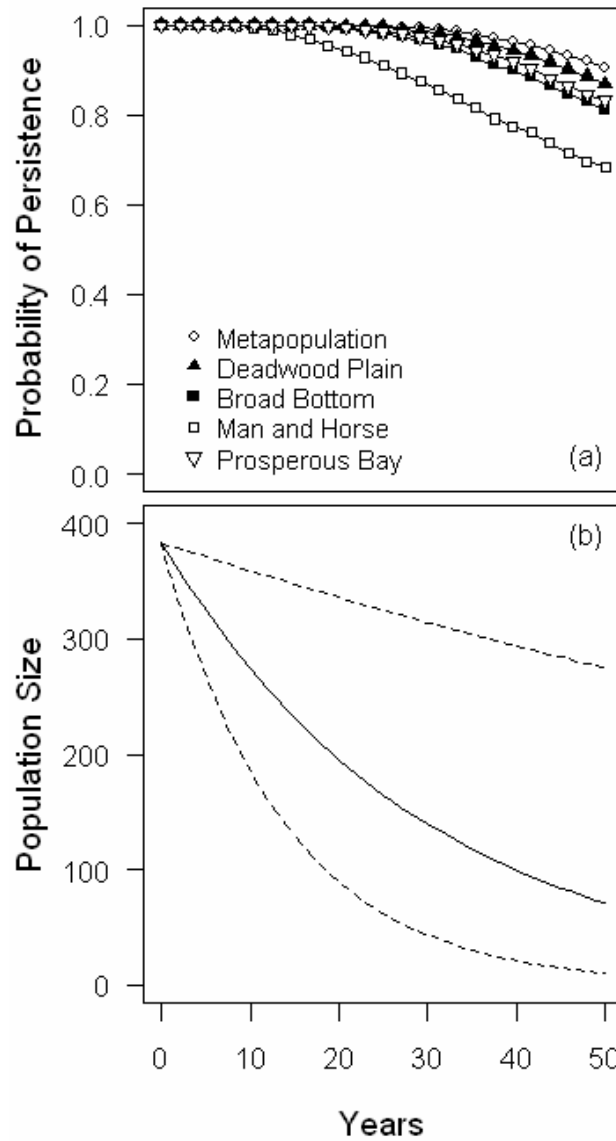
## Results

### *1. Baseline population growth rate and sensitivity analysis*

The distribution of growth rates produced was not normally distributed so non-parametric descriptive statistics are presented. The overall model predicts a slow population decline, median  $r = -0.03381$ , with 90 % of the metapopulations persisting (Figure 2b, 2a). As we modelled starting conditions using the distribution of the parameter estimates rather than the point estimates, the variance around the median growth rate is large ( $s^2 = 0.001664$ , IQR = 0.06627). Persistence varies between sites; the Deadwood Plain population persists 86 % of the time compared to only 67 % at Man and Horse.

The number of nesting attempts  $\text{pair}^{-1} \text{ year}^{-1}$  had the strongest influence on population growth rate (Fig. 3b, Table 3) during the error sensitivity simulation. The other parameters have small influences on  $r$  when varied across their respective confidence intervals and sampling error in these parameters is unlikely to appreciably alter the conclusions drawn from the population model. Adult survival had the strongest influence on population growth rate out of the four demographic parameters, even though its confidence interval was forty times smaller than that of brood survival (Figure 3a). The other three parameters had a similar influence when varied across their confidence intervals. There were significant second order interactions, the most powerful being the positive interaction of nest survival and brood survival. Two third-order interactions also explained a significant amount of variation. Care must be taken when interpreting these model results as p-values are influenced by the number of replications used and are thus most usefully used comparatively.

A weak positive relationship was found between population growth rate and starting metapopulation size (slope  $= 3.593 \times 10^{-4}$ ). However, starting metapopulation size does not appear to be an important determinant of growth rate over the range of values tested as only 1 % of variation in growth rate was explained by this relationship.



**Figure 2** – (a) probability of persistence over 50 years for the metapopulation and each site population. (b) projected metapopulation size, using the median growth rate, and the 1<sup>st</sup> and 3<sup>rd</sup> quartiles of the distribution.

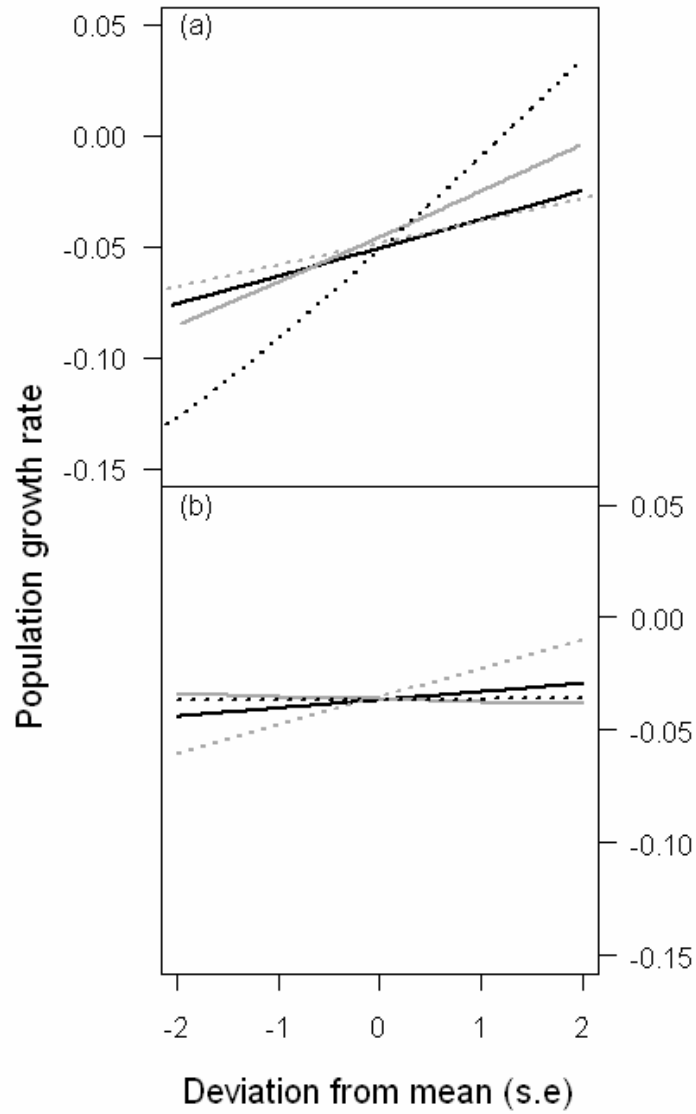


**Table 3** – *Explanatory variables of population growth rate (response variable) using linear regression*

<i>Error sensitivity</i>		Adjusted R-squared: 0.8264		
	Estimate	S.E	t-value	P-value
Intercept	-0.06288	0.002258	-27.852	< 0.001***
Incubation Period	-0.006928	0.002189	-3.165	0.0021**
Fledging Period	-0.002238	0.001871	-1.196	0.2347
Nests per Year	0.05055	0.002454	20.599	< 0.001**
Fledglings per Brood	0.01433	0.002223	6.446	< 0.001***

<i>Demography sensitivity</i>		Adjusted R-squared: 0.9472		
Intercept	-0.04157	0.001556	-26.714	< 0.001***
Brood Survival	0.02642	0.002350	11.240	< 0.001***
Nest Survival	0.03662	0.002541	14.410	< 0.001***
Adult Survival	0.06916	0.002315	29.870	< 0.001***
Juvenile Survival	0.02322	0.002935	7.913	< 0.001***
Brood: Nest	0.01350	0.004274	3.159	0.002179**
Brood: Adult	-0.007075	0.003708	-1.908	0.0597.
Nest: Adult	-0.003510	0.003746	-0.937	0.3513
Brood: Juvenile	0.005500	0.004108	1.339	0.1841
Nest: Juvenile	0.003637	0.004604	0.790	0.4317
Adult: Juvenile	-0.01065	0.004746	-2.245	0.02732 *
Brood: Nest: Adult	-0.03092	0.006167	-5.01	< 0.001 ***
Nest: Adult: Juvenile	-0.02428	0.006924	-3.506	< 0.001 ***



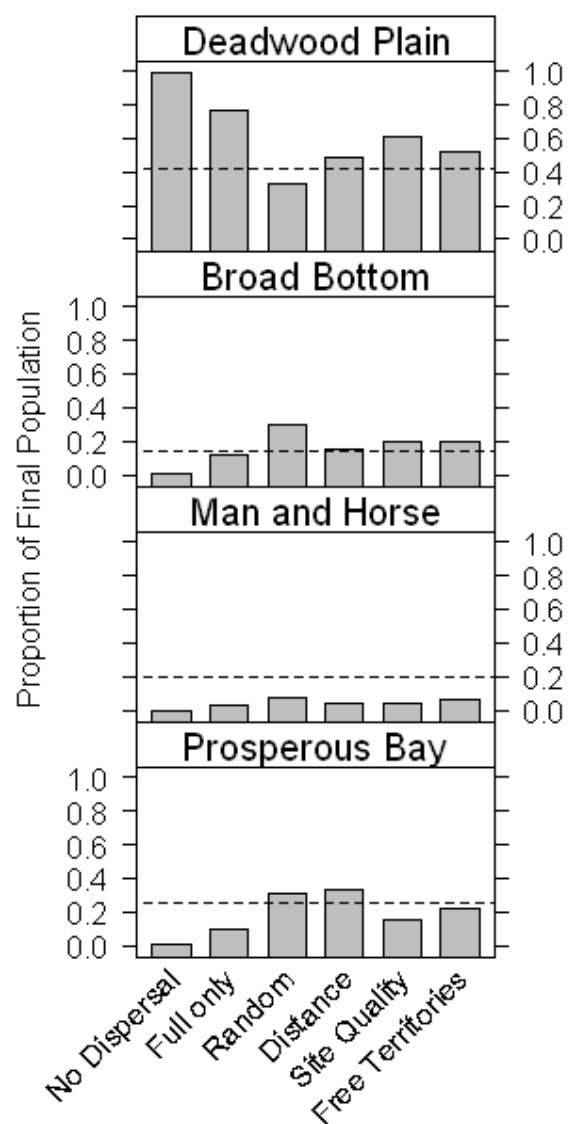
**Figure 3** – Sensitivity analysis, (a) demographic parameters, Key: Brood survival – black; Nest survival - grey; Adult survival - black dotted; Juvenile survival - grey dotted: (b) life-history parameters, Key: Fledglings brood<sup>-1</sup> - black; Nesting period – grey; Fledging period - black dotted; Nests pair<sup>-1</sup> year<sup>-1</sup> - grey dotted.

## *2. Dispersal between sites*

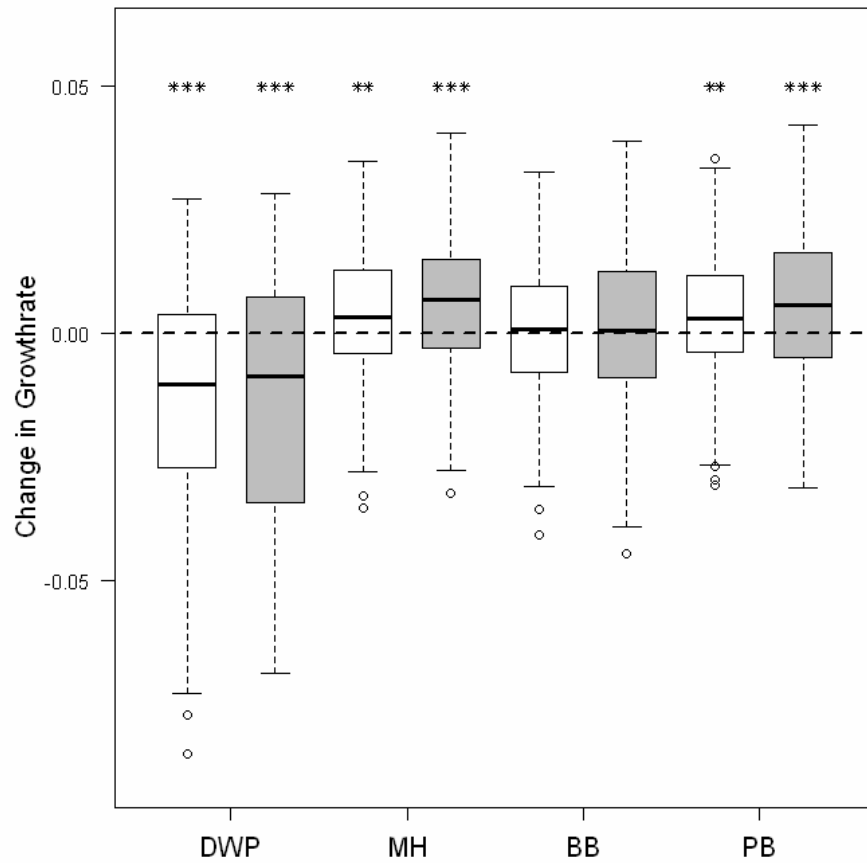
The different dispersal options led to significantly different estimates of  $r$  (Table 4), and they also differed in how the final metapopulation was distributed across the sites (Figure 4). The highest growth rate was found where there was no dispersal between sites and the lowest where dispersal was random. However, the no dispersal simulation ended with over 90 % of the metapopulation in one site, Deadwood Plain. This is neither realistic nor desirable, as over the past twenty years although population size at each site has varied extinction and re-colonisation have been rare. Dispersal therefore appears to be key to the persistence of the metapopulation. Consequentially, dispersal options which result in sites retaining similar proportions of the metapopulation compared to starting conditions would seem plausible. Options 4-6 meet this criterion better than the others when the standard deviation from the starting proportions are calculated.

## *3. Site removal*

The population growth rate was significantly reduced when Deadwood Plain was removed from the simulation, but not so when any of the other site was removed (Figure 5, Table 4). Indeed the growth rate increased when Man and Horse or Prosperous Bay was removed, although the large error bars around the estimates suggest that the effects may not be substantially distinct. When site removal was combined with habitat improvement at the remaining sites there was little overall improvement in growth rate ( $t_{2398} = -1.189$ ,  $P = 0.235$ ), and growth rate remained above starting conditions for Man and Horse and Prosperous Bay only and was still significantly depressed when Deadwood Plain was the target site.



**Figure 4** - Distribution of birds in final metapopulation between sites for each dispersal option, dashed line indicates the proportion of birds in each site at present



**Figure 5** – Deviation from baseline growth rate during site removal simulation. The site that was removed is indicated on the x-axis, white indicates site removal, grey, site removal plus compensatory habitat improvement elsewhere.

**Table 4** – *Linear regression for dispersal and site removal simulations, response variable, growth rate (r).*

<i>Dispersal</i>		Adjusted R-squared: 0.8462		
	Estimate	S.E	t-value	P
No Dispersal	0.0005782	0.0008896	0.650	0.516
Site Full Only	-0.001287	0.001258	-1.023	0.307
Random	-0.058799	0.001258	-46.734	< 0.001***
Distance	-0.03391	0.001258	-26.956	< 0.001***
Site Quality	-0.01972	0.001258	-15.671	< 0.001***
Free Territories	-0.03828	0.001258	-30.422	< 0.001***

<i>Site Removal</i>		Adjusted R-squared: 0.1354		
Control	-0.03006	0.0008402	-35.773	< 0.001***
Deadwood	-0.01191	0.001188	-10.023	< 0.001***
Broad Bottom	0.0009655	0.001188	0.813	0.4166
Man and Horse	0.003783	0.001188	3.184	0.00148**
Prosperous Bay	0.003713	0.001188	3.124	0.00182**

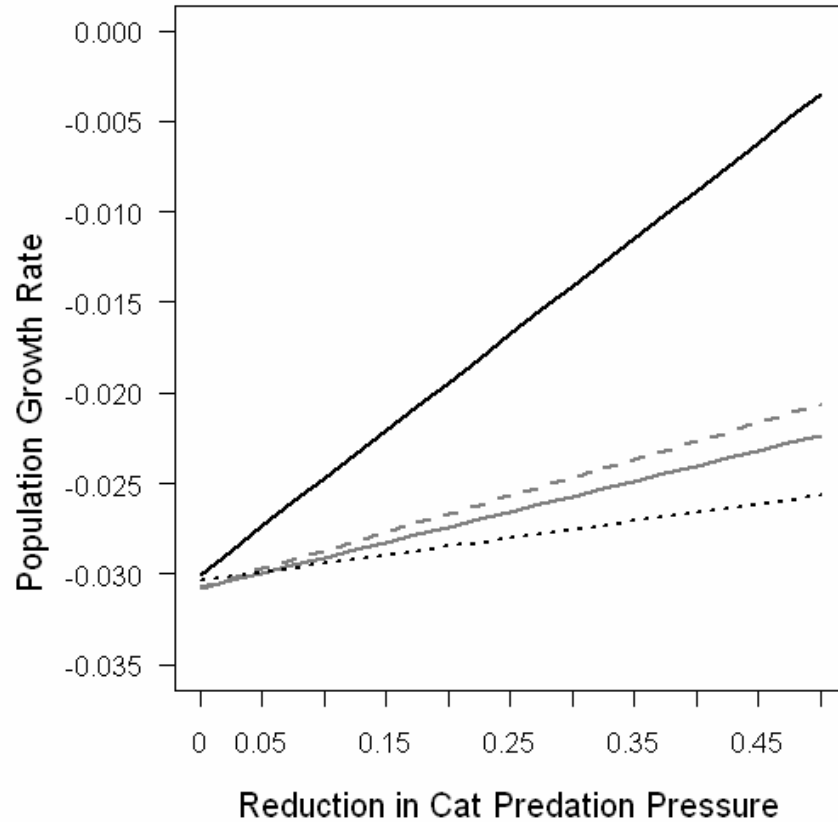
  

<i>Site Removal plus additional habitat</i>		Adjusted R-squared: 0.1424		
Control	-0.03006	0.0009636	-31.191	< 0.001 ***
Deadwood	-0.01298	0.001363	-9.526	< 0.001 ***
Broad Bottom	0.001752	0.001363	1.286	0.199
Man and Horse	0.005859	0.001363	4.299	< 0.001 ***
Prosperous Bay	0.005372	0.001363	3.942	< 0.001 ***

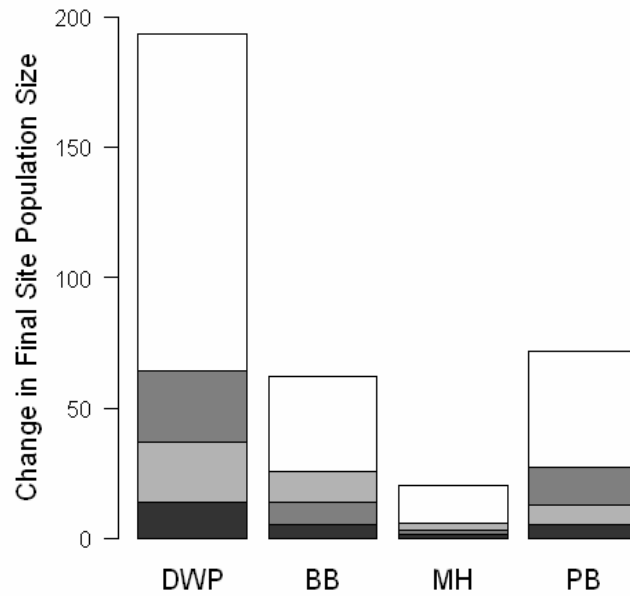
#### *4. Conservation Management Options*

Site level cat control has variable benefits. Counter-intuitively an increase in productivity at the site which currently has the highest survival to adulthood, Deadwood Plain, has the greatest benefit to the metapopulation (Figure 6, Table 5). From Figure 7 we can see how reducing predation pressure influences the final population size in each population. It is clear that cat control at Deadwood Plain would be beneficial to all populations not just its own, leading to the greatest population increase at all sites. Nevertheless, population growth rate remains below zero for all options where control is

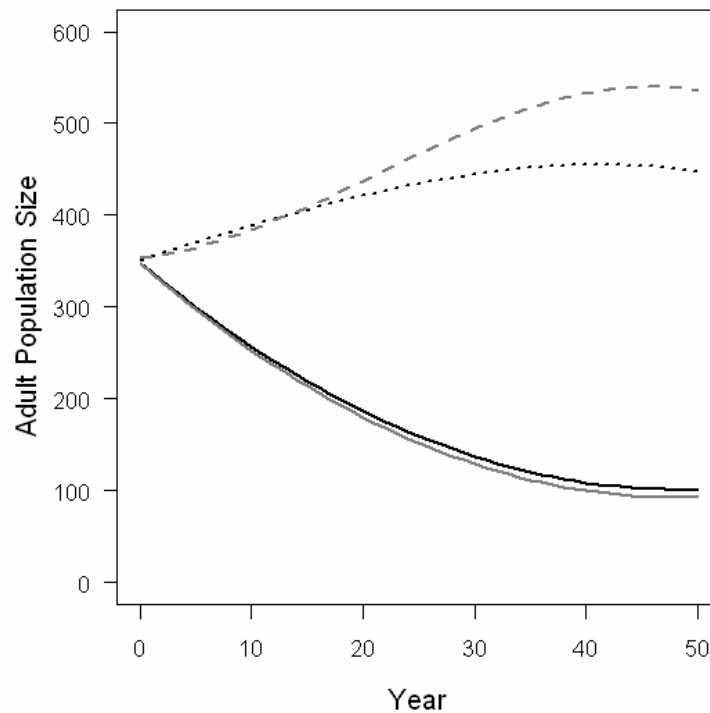
carried out at one site only, indicating that two or more sites would need to be targeted for the population to substantially increase. Figure 8 shows the results of island wide conservation, where the interaction of habitat improvement and predator control is very clear, as the population growth rate increases due to reduced predation the benefit of habitat improvement also increases. Currently there appears to be no benefit of indiscriminately providing additional habitat at all sites.



**Figure 6** - Relationship between site specific reduction in nest predation pressure and population growth rate. Key: DWP - black; BB – grey; MH - dotted black; PB - dashed grey.



**Figure 7** - Change in site level population size at year 50 compared to that estimated using baseline conditions. Key: DWP controlled - white; PB controlled - light grey; BB controlled - mid-grey; MH controlled - dark grey.



**Figure 8** - Conservation management over the whole metapopulation. Key: Baseline conditions - black; extra 0.5 km<sup>2</sup> of habitat at each site - grey; 0.5 reduction in cat predation pressure at all sites - black dotted; both predator control and extra habitat - grey dashed.



**Table 5** – ANOVA output of Conservation management simulations: response variable = growth rate ( $r$ )

<i>Site level management</i>		Adjusted R-squared: 0.2503		
	Estimate	S.E	t-value	P
Baseline	-0.0299402	0.0005596	-53.502	< 0.001***
Deadwood + cat control	0.0131924	0.0004748	27.783	< 0.001***
Broad Bottom + cat control	0.003721	0.0004748	7.836	< 0.001***
Man and Horse + cat control	0.002080	0.0004748	4.381	< 0.001***
Prosperous Bay +cat control	0.004564	0.0004748	9.611	< 0.001***

<i>Island wide Management: transformed</i>		Adjusted R-squared: 0.725		
Baseline	0.01293	0.0002659	48.649	< 0.001***
Predator control	0.006943	0.0001880	36.930	< 0.001***
Habitat improvement	-0.0009488-	0.0003760	2.524	0.0117*
Interaction	0.001050	0.0002659	3.951	< 0.001***

## Discussion

### *Model structure*

Incorporating stochasticity is known to decrease the long run population growth rate (Lande 2002), however, depending on the type of variation this is not always the case (White 2000). White discusses four aspects of variation: demographic, environmental (including temporal and spatial) and individual. Demographic and temporal variation are seen to decrease the chance of population persistence, and spatial and individual variation have the opposite effect. This is because the latter two reduce demographic auto-correlation between sites and individuals, so not all areas or individuals have a bad year synchronously, thus dampening overall annual variation. Whereas, if vital rates show temporal auto-correlation increasing temporal variation would extenuate the peaks and troughs of good and bad times. Due to insufficient data our model does not include individual variation and contains a single parameter controlling environmental variation, which exhibits neither temporal or spatial auto-correlation nor covariance amongst demographic rates. Omitting these complexities will be partially mitigated as their effects are antagonistic. However since their magnitudes are unknown we cannot

predict the net effect. The discussion so far has been restricted to process variation; however, demographic estimates will also include sampling variation, and because of this some authors have asserted that total variance is often overestimated (Gould and Nichols 1998). Assessing process variation requires lengthy data series and short studies like ours tend to underestimate actual variation (Pimm 1991, cited in Beissinger 2002), therefore removing all sampling variation could underestimate total variation (Ludwig 1999). Programme MARK (White and Burnham 1999), which was used to calculate most of the demographic parameters in our model includes a shrinkage factor to attempt to more accurately assess process variation only (White et al. 2002).

Apart from an upper limit on the number of territorial pairs in each site no density dependence was included in the model. This is because the carrying capacity of each habitat area is uncertain and therefore it is difficult to assess how density dependence is currently influencing the metapopulation. There was no consideration of genetics in the model, largely due to the absence of any genetic analysis of the species to date. There are however, several reasons to suppose that the negative genetic effects of small population size may be minimized in this case. Firstly, there is a single metapopulation rather than many isolated populations. Secondly, the manifestation of inbreeding depression on infertility or embryo death appears to be lower than the average amongst species recovering from small population sizes (FB, unpublished data, Heber and Briskie 2010). Finally, it is likely that St. Helena Plovers have always had a relatively small population size and therefore the genetic load may be lower than in other species.

### *1. Baseline simulation and sensitivity*

Population viability analysis is unlikely to give an accurate absolute prediction of population growth rate. However, if the distribution of demographic estimates is used as starting conditions rather than simply the point estimate we can get an idea of the distribution of potential growth rates. Nevertheless, the resulting confidence intervals are often large and it can be difficult to test the model or use it to make robust predictions. Although various ways of testing stochastic population models have been proposed (Lindenmayer et al. 2000; McCarthy et al. 2001), it remains a challenging task and at present we do not have sufficient data in order to do so. Annual census counts for the St. Helena Plover metapopulation have remained between 300-400 individuals for the past five years (SHNT 2011), however, year to year variation is large and no

clear trend is present. Moreover, since we only have one metapopulation, model testing will always be difficult, since what we observe is simply one realization from a whole distribution of possibilities and outliers would be expected from time to time.

Sensitivity analysis can serve several functions. By highlighting those parameters most influential to population persistence it indicates: where accurate estimation is critical, the influence of sampling error, and importantly, targets for conservation management. However, demographic parameters that have high sensitivities tend to have low variability or are difficult to alter through management (Norris and McCulloch 2003; Wisdom et al. 2000), and are therefore not necessarily the best targets for conservation. Alternative methods of sensitivity analysis were proposed to address this issue, for example relative sensitivities or logistic regression (Cross and Beissinger 2001; Mills and Lindberg 2002; Wisdom et al. 2000). Our approach was to compare the influence of varying parameters across their respective confidence limits, akin to their natural variation, rather than altering parameters by an equal amount or percent. The method used is most similar to the logistic regression approach, differing only in the response variable used in regression analysis (population growth rate compared to a binary value - extinct or persisted). Although this gives a more realistic idea of how influential each parameter is, and gives a starting point from which to design management actions from, it does not address how different parameters would respond to management. Norris & McCulloch (2003) argued that given this restriction what they termed ‘scope of management analysis’, aimed at linking a conservation action to an associated change in demographic estimate, would be more useful.

Altering daily adult survival explained the most variation in the population growth rate (Table 3). This is very common in sensitivity analysis of waders (Dinsmore et al. 2010; Hitchcock and Gratto-Trevor 1997; Ottvall and Hårdling 2005; Plissner and Haig 2000), although it is not universal (Keedwell 2004). However, it is very difficult to compare different studies due to the different methods of sensitivity analysis used and life history parameters included. Dinsmore *et al.* (2010) conducted a similar analysis to ours in addition to classic elasticities. They investigated the influence on the population growth rate of increasing each vital rate in turn from the mean to the maximum observed; this latter analysis gave chick survival to be the most influential parameter as opposed to adult survival in the elasticity analysis, however it is likely that an imprecise estimate of

chick survival was partly responsible for this outcome. In general, unless there is significant predation upon adults, management actions for waders have not targeted this life stage. Elsewhere, we found adult survival lower at Man and Horse than other areas, implying potential for increase through management. There could be several reasons why adult survival is poor at this site. It has the highest relative cat density and lowest productivity (Burns 2011, Chapter 2). Therefore, there could be direct predation on adults, or adults could be investing more into reproduction than elsewhere.

Alternatively, birds at this site may be of poorer quality and in this latter case conservation management is unlikely to increase adult survival. The life history parameters used in the error sensitivity analysis were those where estimates were made on limited data, in particular estimating the number of breeding attempts a pair has per year is labour intensive and our results are based on one year of data only. Variation across each parameter's range showed in general small changes in population growth rate. The number of breeding attempts per year showed the highest sensitivity value. Nevertheless, this parameter is expected to vary with the success of breeding attempts and is therefore likely to decline with conservation management rather than increase.

## *2. Dispersal*

The importance of dispersal in population dynamics is well known, as is that of incorporating behavioural mechanisms conditional on individual experience or state rather than fixed percentages or simple diffusion (Bowler and Benton 2005; Reed 1999). Although the subject of much recent empirical and theoretical work, it is widely acknowledged that dispersal is a multi-causal process, and as such few general rules have emerged (Bowler and Benton 2005; Byholm et al. 2003). The majority of previous work has focused on some aspect of patch quality, whether the natal site, inter-site habitat or recipient site. Many proximal mechanisms influencing dispersal have received some support in the literature, for example density dependence (Matthysen 2005), sex ratio (Wilson and Arcese 2008), patch size and isolation (Wilson and Arcese 2008), food availability (Byholm et al. 2003), and conspecific productivity (Danchin et al. 1998). For a fuller discussion of the recent literature see Bowler & Benton (2005).

One of the benefits of our model is that we can see in detail the patterns of emigration and immigration resulting from each dispersal option, thus allowing us to investigate whether various rules of dispersal fit observed patterns, following the methods of

pattern orientated modelling (Grimm and Railsback 2005; Grimm et al. 2005). Pattern orientated modelling attempts to use simple behavioural rules to recreate the complex patterns observed. This is a useful modelling approach, as understanding the underlying behaviour can allow the outcome of a novel set of conditions to be predicted (Norris 2004). The main drawback to this approach in our case is the paucity of data currently available on dispersal patterns for the St. Helena Plover, which therefore means that we cannot differentiate between all of the dispersal rules tested in the model. From resighting records it would appear that, similar to other species (Breininger 1999; Byholm et al. 2003), young birds make prospecting visits to other sites, in particular those in close proximity to their natal site. It would therefore appear that they are using some cues of habitat quality both in the natal site and at others to decide where to settle. This makes the rule based strictly on distance between sites less likely, and supports those based on assessing site quality or territory availability. It would appear that at present the influence of dispersal on growth rate is controlled by the net emigration from one site, Deadwood Plain. This site has a positive population trajectory in isolation but cannot sustain this with increasing levels of emigration. When dispersal is allowed this site is a source population, and, although this serves to homogenize the population density across sites and delay any sites going extinct, it leads to a lower population growth rate in the long run. This pattern of dispersal is very likely to be conditional on the population growth rate and indeed we find that as soon as productivity is increased at Deadwood Plain it can afford to be a net exporter without detriment to its own population (Fig. 7).

### *3. Site removal*

Population growth rate was significantly depressed when Deadwood Plain was removed, even if additional habitat was provided at the remaining sites. As well as highlighting the importance of Deadwood Plain this result shows that in order to be fully compensatory, habitat provided as mitigation for development must be of equal or greater quality to that removed. Moreover, creating additional habitat in areas of low productivity may actually suppress growth rate, as it encourages young birds to recruit into sink habitats, in particular when dispersal decisions are based on the number of available territories (Dispersal option 6). In our simulation additional habitat was created within current St. Helena Plover distribution so no new populations were established. However, if habitat is created in new areas then it is unknown how quickly,

or if, birds would colonize, as many species are more likely to settle in areas where conspecifics are already present due to conspecific attraction (Matthysen 2005). New areas would have to be monitored carefully and if necessary efforts made to attract birds to settle.

#### *4. Conservation management*

Invasive species are thought to have been the key cause of past extinctions of island bird species (Blackburn et al. 2004; Johnson and Stattersfield 1990), and although other threats now compete for this role they remain a major risk to species persistence (Brooke et al. 2007; Hilton and Cuthbert 2010). There is general agreement that a small set of mammal species, including two nest predators of the St. Helena Plover, cats and rats, have had a disproportionate role in past extinctions and current endangerments (Courchamp and Chapuis 2003). Predator control at Deadwood Plain gives not only the greatest increase in the final island population size compared with control at any of the other sites, but also the highest population size at each site. Although numerically optimal this may not be the best solution overall as it leaves the global population heavily dependent on a key source population and vulnerable to future change in that area. Simulating island wide cat control showed great benefits to the metapopulation from relatively small decreases in predation pressure (Fig. 8). The cat control simulations presented here assume that there would be no numerical response from other species, for instance rats and rabbits. Empirical and theoretical studies would, however, suggest that this is unlikely (Bergstrom et al. 2009; Courchamp et al. 1999a; Courchamp et al. 1999b), but see Bonnaud et al. (2010). Food web interactions were not included in the model at this stage as they are complex and difficult to predict (Courchamp and Chapuis 2003). Assessing the consequences of cat control is a priority area for further work, however. Although predator control appears beneficial, it would only increase the metapopulation size to that which would fill the available habitat, which is predicted to only allow for around 600 individuals. Although MVP (minimum viable population) is a concept that has fallen out of favour due to difficulties in estimation, it is pertinent to note that two recent reviews have both cited average critical figures of several thousands (Reed et al. 2003; Traill et al. 2007). Therefore, maintaining current suitable habitat is unlikely to be sufficient to ensure the long-term resilience of the metapopulation.

The results of the predator control and habitat improvement simulations crucially depend on assumptions on how the environment is influencing demography. Although previous research has found no influence of habitat quality on nest survival, the data used were observational rather than experimental and therefore small effect sizes may have been overlooked (Burns 2011, Chapter 3). These simulations address only the biological response of the metapopulation, social and political aspects, as well as cost will also have to be taken into consideration before deciding a course of action (Baxter et al. 2006; Ratcliffe et al. 2005). For example, some populations are close to villages, and so lethal control of cats may be unacceptable in these areas.

### *Conclusions*

The global population of St. Helena Plover was predicted to be declining slowly, with a high chance of persistence over the timeframe simulated. In common with many other studies we found adult survival to have the greatest influence on model output, with potential to increase this parameter at one site: Man and Horse. Reducing predation from cats was found to benefit the species and doing so in conjunction with habitat improvement had greater than additive benefits. One site, Deadwood Plain, was seen to be vital to the metapopulation; it has currently the largest population and has the highest survival to adulthood. As such it is a net exporter of young birds and removing it is predicted to have greatest negative impact on the metapopulation. Although St. Helena Plovers are protected by law from direct persecution there is no protection of land used by them. It is strongly recommended that key sites, including Deadwood Plain are protected. Protective measures should include provision for management and monitoring. To avoid reliance on one or two source sites, however, work needs to be done to bring other areas up to appropriate standards in order to increase the resilience of the metapopulation. It is likely that several areas used by St. Helena Plovers will be subject to development in the coming years, and therefore a minimum policy of no net loss of plover habitat through development is highly recommended.

The model indicates several directions for further work. Firstly, trials of predator management coupled with a more detailed assessment of the influence of the predators on demography, and the influence of habitat characteristics on predator numbers. Secondly, patterns of dispersal influence population growth rate and interact with vital rates. A fuller understanding of the mechanism of natal dispersal would therefore be

useful. Thirdly, collection of adult survival data should be continued in order to refine this crucial model parameter. Finally, it is likely that variables such as climate and prey availability also influence demography and contribute to annual variation. It would be informative to try to quantify these relationships as this would increase the predictive value of the model (Jonzén et al. 2010). Data collected through these facets of further work could then be used to update and refine the population model.

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## Conclusions

Although the research described in this thesis focussed on the specific topic of understanding the conservation biology of the St. Helena Plover, the results presented will also be more broadly applicable to the fields of conservation biology and population biology. The key findings of the research are summarised below, followed by a discussion of the questions provoked by this work and some important areas for future work.

### *Current status of the St. Helena Plover*

The population model (Chapter 6) predicted that the numbers of St. Helena Plover would decline slowly if conditions remained unchanged, but that there was a high chance of the species persisting for the next 50 years. The population model also highlighted the reliance of the meta-population on one site, Deadwood Plain. This area has currently the greatest concentration of birds and the most favourable demographic rates. It is a net exporter of fledglings to other areas of the island, which serves to stabilise the distribution of birds across the island. Moreover, simulations suggested that overall population growth rate would decline significantly if this site were to be removed through development.

### *Parameters influencing the distribution and demography of the St. Helena Plover*

Predation: St. Helena Plover nests were predated by a range of species that have arrived on the island since its discovery by humans. Cats were the most important nest predator and cat densities were strongly correlated with spatial variation in nest survival. It is likely that predator densities are preventing populations at some sites from producing sufficient fledged young to balance out adult mortality, and that these populations rely upon immigration to maintain stable populations. Additionally, food availability may limit productivity, and the magnitude of this effect may vary with predator abundance (Chapter 2). Nevertheless, adult St. Helena Plovers have retained effective anti-predator behaviours, and have done so in the absence of native nocturnal predators. Adult survival is high, and male plovers do not appear to suffer elevated mortality even though they incubate throughout the night, which is the active period of the majority of nest predators currently present. However, survival may be suppressed when predators

are numerous; the site with the greatest predator densities also exhibited the lowest adult survival (Chapter 4).

Habitat: Habitat characteristics appear to be dictating the distribution of breeding territories rather than local breeding success. Nest survival, chick survival and chick growth were not influenced by habitat variables (Chapters 3, 4). Areas selected for breeding territories were characterised by short vegetation, low or no shrub cover and a shallow slope. This suggests that the plovers are selecting breeding habitat in order to maximise visibility from the nest. In pasture areas short vegetation is also likely to increase the accessibility of the plovers' invertebrate prey; in particular for chicks. Habitat suitability was heterogeneous within and between sites, but the total area of suitable habitat appeared to be greater than that required to support the current population. However there may be other factors not considered here that would reduce the attractiveness of otherwise suitable areas. Habitat change over time at one site, Deadwood Plain, explained a substantial amount of the observed change in bird densities, indicating that habitat deterioration played a part in the recent decline in population size of this species. However, it is likely that other factors were also involved (Chapter 3).

#### *Assessment of conservation techniques and management options*

Despite increasing nest survival in several other species, nest exclosures were not an effective conservation technique for the St. Helena Plover. Exclosure use did not increase nest survival and was associated with increased adult mortality. The predicted population level impact of exclosure use was negative (Chapter 5). The use of engraved leg flags as a way of individually marking St. Helena Plovers was not as efficient for re-sighting as the use of a series of three colour rings. It is likely that leg flags would be more useful for species where the birds form large flocks (Chapter 1).

Simulations indicated that reducing predation pressure from cats would greatly benefit the population and allow it to increase. There was a greater than additive benefit of conducting habitat improvement at the same time as predator control, but habitat improvement in isolation provide little benefit, particularly in areas of low productivity. Deadwood Plain is a potential target for conservation intervention, as predator control here resulted in the largest increase in population growth rate when control was simulated at each site in turn. However, to avoid dependence upon one breeding site

other areas should also be improved. A key target would be Man and Horse, as predator control at this site may not only increase productivity, but also increase adult survival. This could greatly benefit the species, as sensitivity analysis indicated that adult survival has the greatest influence on the population growth rate (Chapter 6).

#### *Broader applications of the research*

The ecology of the St. Helena Plover is relatively unknown and therefore my research adds to the body of knowledge relating to *Charadrius* species, and to waders in general. The results presented here will be useful for comparative studies. The ancestral St. Helena Plovers are thought to have arrived on the island at least several thousand years ago. Given the paucity of predaceous native species on St Helena it is unexpected that the adult survival of the plover remains high in the presence of several introduced predator species. This finding reminds us that island species do not necessarily lose anti-predator adaptations even after long isolation. Nevertheless, my research highlighted the continued role of introduced predators in the endangerment of island species and gave further evidence that a select few species are having hugely negative impacts when introduced to novel environments. That cats were the most important nest predator in this system was unexpected. High densities of cats are present in many island ecosystems, as well as in association with centres of human population globally. Therefore, the role of cats in limiting the nest survival of ground nesting birds in general may currently be underestimated. My research questions the usefulness of nest exclosures as a conservation management technique. It suggests that the most common design of exclosures is ineffectual at excluding cats, and adds to the increasing body of evidence indicating that exclosures are associated with elevated adult mortality.

Although the inclusion of behavioural decision making rules is well known in individual based modelling, it is not common in population models used to predict population trajectories or to assess probability of species persistence. The addition of behaviour into population models is important as it allows an assessment of the population response to conditions not experienced in the past, for instance predicting species responses to much altered climatic conditions. An important aspect of the conservation management simulations in the population model is that they were based on empirically derived estimates of how the demography may respond to change in the environment. In many other population models these estimates are based on the



subjective opinion of the study authors. Although including these observed relationships is advantageous, our understanding of how environmental parameters influence demography remains limited, reducing the reliability of our model predictions. This criticism is not specific to my study, rather it is a general weakness of population models. An experimental approach to assessing links between demography and environmental change may be advantageous.

### **Future work**

My research here has indicated several areas for future study, three of the most pertinent are discussed below.

#### *Understanding the implications of reducing feral cat populations*

The simulations conducted using the population model assume that there is no numerical response from other species when cat density is reduced. However, recent theoretical and empirical work suggests that this is unlikely to be the case (Bergstrom et al. 2009; Courchamp et al. 1999a; Courchamp et al. 1999b). The nest predators of the St. Helena Plover contain both apex predator (cat) and mesopredator (rat) and therefore the benefit of cat control may be partially or completely negated by an increase in the rat population. Additionally, feral cats are likely to currently limit the population sizes of two other introduced mammals; mice and rabbits. These species currently threaten several of St Helena's endemic invertebrates and plants (Ashmole and Ashmole 2000; Bell and Floyd 2009), therefore any population increase should be avoided. One possible conservation option is feral cat eradication and strict control of the domestic population. Cats have been removed from islands of a similar size to St Helena, however, not from any with such a substantial human population (Oppel et al. 2011). Furthermore, due to the potential ecosystem level responses resulting from cat removal described above, the total removal of feral cats may not be desirable, even if it were possible. Long term control of cats, and potentially one or more of the other species, would be an alternative conservation strategy. For ethical and financial and reasons it would be imperative to undertake the minimum control required to achieve a larger, stable population of St. Helena Plovers. In order to accomplish this, a series of carefully designed and monitored experiments are needed. One possible approach would be a before and after design, assessing the response of the plover population, and that of the

other introduced species (rat, mice, rabbits), to a decrease in cat densities. Based on these experimental results other layers of control could be added if necessary.

*Understanding the interactions between habitat characteristics, food availability and predation*

Predator control remains a controversial issue and projects should be able to demonstrate both a substantial expected benefit and a high probability of success. There is a large and predominately unregulated domestic cat population on St Helena and this may reduce the success of cat control, either due to public opposition or through continued supplementation of the feral population by the domestic. Investigating ways to reduce the impact of predators that do not require ongoing predator control is therefore of great importance, both here and for conservation in general. A recent review of predation in birds called for more research into the ways in which habitat management could reduce the impact of predators (Gibbons et al. 2007).

Although not found in our present analysis, habitat characteristics in the wider area around nesting sites are likely to influence productivity by mediating predator numbers, and by providing cover for approaching predators. These ideas could be investigated by observing natural variation in parameters such as, distance to site edge, or distance to patches of shrub. An experimental approach which manipulates the habitat is likely to prove more informative, however. Nest and brood survival could be monitored at a series of control and treatment sites before and after habitat manipulation. In our research, food availability was predicted to be limiting the total number of nesting attempts a pair had in a year. An experiment could be carried out to manipulate food availability, with the hypothesis that productivity would increase with food availability. The increase in productivity may be direct; an increase in the total number of eggs a female can lay, or indirect; through a reduction in nest predation. In the latter case increased food levels may allow the birds to be away from the nest for less time, or the improved condition of well fed individuals may facilitate more effective anti-predator behaviours.

*Investigating the population level effects of conservation techniques*

Our work is amongst several recent studies that have highlighted the need to assess the efficacy of conservation techniques at a population level. For instance, exclosures have

been observed to increase nest survival but their influence on population numbers remains largely unknown (Smith et al. 2011). One long term study found no increase in population size from the use of exclosures (Neuman et al. 2004). Therefore significant time and money is being spent on actions that may not be benefiting the population. This not only means that we are failing in our goals for conservation, but that we are inefficiently spending the limited financial resources available for conservation. A related issue is the need for a greater focus on quantifying the expected benefits of conservation interventions, as these may be markedly different from initial expectations. In our research nest exclosures were only expected to increase nest survival by 14 % even if half of all nests were protected. In many cases the information necessary to make these calculations is unavailable and here it may be argued that any conservation intervention that would benefit the species should be attempted. However, even limited information can indicate the level of effort required to achieve an observable effect, or to meet conservation targets, and can therefore inform experimental design and allow a more meaningful comparison of alternative conservation options.

More generally, conservation interventions have historically been poorly monitored and the evidence of their efficacy is often lacking (Sutherland et al. 2004). Although work has begun to address this issue, such as the Collaboration for Environmental Evidence (Anon 2010) and Conservation Evidence (Sutherland 2010), a continued focus upon justifying our actions is necessary. This will help to convince others of the value of our work, for instance funding bodies and governments. More importantly it will also improve our success rate, which is clearly imperative when global targets for biodiversity conservation continue to be missed (Butchart et al. 2010).

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## Appendix 1 – Visual Basic code for population model

```

Module Population_model
Sub Main()
    Randomize() : Dim rand As New Random()
    Const Sites As Integer = 4 'number of sites in model

'Define vital rates that will be used in this model.
'NEST SURVIVAL, beta parameters from programme MARK
Const Beta1 As Single = 4.2006749 'dwp
Dim MeanNestBeta(3) As Single : MeanNestBeta(3) = -0.8954727 : MeanNestBeta(1) = -0.4838142: MeanNestBeta(2) = -1.3581679 'pb;bb; mh
Dim SEMeanNestBeta As Single = 0.33974 'mean of the se for the four beta terms
Const NestBDate = -0.0114847: Const NestBAge = 0.0089031 'no variation in these terms
Dim NestDay As Integer : Dim Nest(4, 4) As Integer 'matrix telling nest survival equation which beta terms to use
For i = 1 To 4
    If i = 1 Then Nest(i, 1) = 1 Else Nest(i, 1) = 0 : If i = 2 Then Nest(i, 2) = 1 Else Nest(i, 2) = 0 : If i = 3 Then Nest(i, 3) = 1 Else Nest(i, 3) = 0
    If i = 4 Then Nest(i, 4) = 1 Else Nest(i, 4) = 0
Next i
'CHICK SURVIVAL
Const MeanDailyChickSurvivalAll As Single = 0.97108674
Dim SEMeanDailyChickSurvivalAll As Single = 0.00529087
'ADULT SURVIVAL, beta estimates
Dim MeanDailyAdultSurvivalAll(2) As Single : MeanDailyAdultSurvivalAll(1) = 1.3612179 'for dwp, bb, pbp
MeanDailyAdultSurvivalAll(2) = 1.2291123 'for mh
Dim SEDailyAdultSurvivalAll As Single = 0.04 'just one estimate of se
'JUVENILE SURVIVAL
Dim MeanDailyJuvenileSurvivalAll(2) As Single : MeanDailyJuvenileSurvivalAll(1) = 0.9469325 ^ (1 / 30.417) 'dwp, convert monthly to daily est
MeanDailyJuvenileSurvivalAll(2) = 0.9005398 ^ (1 / 30.417) 'other sites, from model averaging
Dim SEDailyJuvenileSurvivalAll = 0.0006 'average variation / 30

'number of sets of starting conditions needed for each simulation
Dim simulation_number As Integer = 10 : Dim Simulations As Integer
Const Duration As Integer = 50 'number of years each simulation runs for
Select Case simulation_number

```

```

Case Is = 1
    Simulations = 100 ' number of different sets of starting conditions to try
Case Is = 2
    Simulations = 100 'sensitivity analysis error
Case Is = 3
    Simulations = 21 ' size of starting population
Case Is = 4
    Simulations = 6 'dispersal simulation
Case Is = 5
    Simulations = 48 'site removal simulation, plus predator control &/or habitat improvement
Case Is = 6
    Simulations = 27 'predator control, baseline, remove 25% of cats, remove 50% of cats
Case Is = 8
    Simulations = 1 'baseline not including different starting conditions, dispersal =5
Case Is = 10
    Simulations = 12 'habitat improvement and/or predator control, 0.5 km extra at each site plus 50% cat reduction
Case Is = 11
    Simulations = 100 'demographic sensitivity
End Select

Dim OTerritories(Sites) As Integer 'set the carrying capacity of the site, study sites account for 48% of island so times by 2 to mimic whole island
Const OTerritory As Integer = 124 'O specifies original, set to max number of territories at any one site
Dim Territory As Integer = 124 : Dim Territories(Sites) As Integer
OTerritories(1) = 124 : OTerritories(2) = 44 : OTerritories(3) = 44 : OTerritories(4) = 52 : dwp, bb, mh, pb
Dim StatusAll(Territory, Sites) As Integer 'array specifying the current status of each territory, # rows equal to the biggest site
Dim OstartTerr(Sites) As Integer 'number of initially occupied territories
OstartTerr(1) = 80 : OstartTerr(2) = 26 : OstartTerr(3) = 38 : OstartTerr(4) = 48 'dwp, bb, mh, pb
Dim startTerr(Sites) As Integer
Dim Floating(Sites) As Long 'set up floating group, non-breeders
Dim JuvenileAll(1000, Sites) As Integer 'set up juvenile group
Dim ChanceOfAPair(10) As Single 'set up probabilities that there will be a male and female out of a group of specified number
ChanceOfAPair(1) = 1:    ChanceOfAPair(2) = 0.5:    ChanceOfAPair(3) = 0.25:    ChanceOfAPair(4) = 0.125: ChanceOfAPair(5) = 0.0625
ChanceOfAPair(6) = 0:    ChanceOfAPair(7) = 0:    ChanceOfAPair(8) = 0:    ChanceOfAPair(9) = 0:    ChanceOfAPair(10) = 0

Dim detection(Sites) As Single 'correction for <100% nest detection

```

```

detection(1) = 1.322: detection(2) = 1.1666 : detection(3) = 1.3836 : detection(4) = 1.3227 'dwp, bb, mh, pb
Dim ProbNestInitiationAll As Single 'this is the chance of nest initiation on any given day for any given pair, using an array of actual values
Dim NestInitiationWeek(52) As Single : Dim NestInitiationWeek_V As Single
Const Nest_average As Single = 1.96875 : Const Nest_se As Single = 0.2760322 'average number of nests and se, for error sense sim - 2
Dim Nest_correct As Single
NestInitiationWeek(1) = 0.02098102: NestInitiationWeek(2) = 0.01723912: NestInitiationWeek(3) = 0.01430296
NestInitiationWeek(4) = 0.01197588: NestInitiationWeek(5) = 0.01011524: NestInitiationWeek(6) = 0.00861583
NestInitiationWeek(7) = 0.00739892: NestInitiationWeek(8) = 0.00640491: NestInitiationWeek(9) = 0.0055882
NestInitiationWeek(10) = 0.0049136: NestInitiationWeek(11) = 0.00435373: NestInitiationWeek(12) = 0.00388712
NestInitiationWeek(13) = 0.00349686: NestInitiationWeek(14) = 0.00316953: NestInitiationWeek(15) = 0.00289443
NestInitiationWeek(16) = 0.00266301: NestInitiationWeek(17) = 0.0024684: NestInitiationWeek(18) = 0.00230506
NestInitiationWeek(19) = 0.00216854: NestInitiationWeek(20) = 0.00205527: NestInitiationWeek(21) = 0.00196237
NestInitiationWeek(22) = 0.00188755: NestInitiationWeek(23) = 0.00182904: NestInitiationWeek(24) = 0.00178547
NestInitiationWeek(25) = 0.00175583: NestInitiationWeek(26) = 0.00173947: NestInitiationWeek(27) = 0.001736
NestInitiationWeek(28) = 0.00174536: NestInitiationWeek(29) = 0.00176775: NestInitiationWeek(30) = 0.00180367
NestInitiationWeek(31) = 0.00185395: NestInitiationWeek(32) = 0.00191974: NestInitiationWeek(33) = 0.0020026
NestInitiationWeek(34) = 0.00210453: NestInitiationWeek(35) = 0.00222807: NestInitiationWeek(36) = 0.0023764
NestInitiationWeek(37) = 0.00255347: NestInitiationWeek(38) = 0.0027642: NestInitiationWeek(39) = 0.00301471
NestInitiationWeek(40) = 0.00331258: NestInitiationWeek(41) = 0.0036673: NestInitiationWeek(42) = 0.00409072
NestInitiationWeek(43) = 0.00459775: NestInitiationWeek(44) = 0.00520726: NestInitiationWeek(45) = 0.00594322
NestInitiationWeek(46) = 0.00683632: NestInitiationWeek(47) = 0.00792615: NestInitiationWeek(48) = 0.00926421
NestInitiationWeek(49) = 0.01091813: NestInitiationWeek(50) = 0.01297768: NestInitiationWeek(51) = 0.01556361
NestInitiationWeek(52) = 0.01884081

```

'Import an array of juvenile ages and probability of recruitment into the vector, the entry number corresponding to the age of the juv

```

Dim Recruitment(454) As Single : Dim Irow As Integer
Dim oExcel As Object = CreateObject("Excel.Application")
Dim oBook As Object = oExcel.Workbooks.Open("c:\Wirebird\My Dropbox\Data_Files\Analysis\modelling\wirebird_vb_codemultisite13910finalvitals.xls")
Dim oSheet As Object = oBook.Worksheets(1) : Dim DataRange As Object : DataRange = oSheet.Range("AB19:AB269").Value
For Irow = 1 To 251
    Recruitment(Irow + 203) = System.Convert.ToSingle(DataRange(Irow, 1))
Next Irow

```

```

Dim Recruited As Integer : Recruited = 0 'controls whether juvenile birds enter the recruitment loop
Dim Dispersal As Integer: Dispersal = 1 'No dispersal
Dim PartDisp1(10, Sites) As Long 'Controls DispOption 4, 50% natal philopatry, 30% closest other site and 10% each further two sites

```

```

For i = 1 To 10
    If i >= 1 And i < 6 Then PartDisp1(i, 1) = 1 : If i = 6 Then PartDisp1(i, 1) = 2 : If i = 7 Then PartDisp1(i, 1) = 3: If i > 7 Then PartDisp1(i, 1) = 4
Next i
For i = 1 To 10
    If i = 1 Then PartDisp1(i, 2) = 1: If i >= 2 And i < 7 Then PartDisp1(i, 2) = 2: If i >= 7 And i < 10 Then PartDisp1(i, 2) = 3
    If i = 10 Then PartDisp1(i, 2) = 4
Next i
For i = 1 To 10
    If i = 1 Then PartDisp1(i, 3) = 1: If i >= 2 And i < 5 Then PartDisp1(i, 3) = 2: If i >= 5 And i < 10 Then PartDisp1(i, 3) = 3
    If i = 10 Then PartDisp1(i, 3) = 4
Next i
For i = 1 To 10
    If i >= 1 And i < 4 Then PartDisp1(i, 4) = 1: If i = 4 Then PartDisp1(i, 4) = 2: If i = 5 Then PartDisp1(i, 4) = 3: If i > 5 Then PartDisp1(i, 4) = 4
Next i

```

Dim PartDisp2(4, Sites) 'Controls DispOption5: Site Quality, order of sites based on distance from natal site

```

PartDisp2(1, 1) = 0 :    PartDisp2(2, 1) = 3 :    PartDisp2(3, 1) = 1 :    PartDisp2(4, 1) = 2
PartDisp2(1, 2) = 0 :    PartDisp2(2, 2) = 1 :    PartDisp2(3, 2) = -1 :    PartDisp2(4, 2) = 2
PartDisp2(1, 3) = 0 :    PartDisp2(2, 3) = -1 :    PartDisp2(3, 3) = -2 :    PartDisp2(4, 3) = 1
PartDisp2(1, 4) = 0 :    PartDisp2(2, 4) = -3 :    PartDisp2(3, 4) = -2 :    PartDisp2(4, 4) = -1

```

Dim ASAll As Integer 'defines whether adult survival is elevated in any simulation or not

Dim SumStatus(4, Sites) As Integer 'the number of each type of territory, 1=empty, 2 = unmated breeder, 3 = non-breeding pair, 4 = breeding pair

Dim FreeT As Integer : FreeT = SumStatus(1, 1) + SumStatus(1, 2) + SumStatus(1, 3) + SumStatus(1, 4) 'Number of free territories

Dim PropFree(Sites) As Single 'Proportion of a site unoccupied, used in DispOption 6, Free territories

Dim ZeroSite As Integer = 10 'which site is to be removed, for simulation 5 only

Dim Occupied(Sites) As Integer 'how many occupied territories are there? status 1+2+3

Dim NestSum(Sites) As Integer 'how many nests are laid overall?

Dim BroodSum(Sites) As Integer 'sum total of all broods hatching in one year

Dim ChickSum(Sites) As Integer 'sum total of all chicks hatching in one year

Dim SumSuccessfulBroods(Sites) As Integer 'sum total of all broods fledging in one year

Dim FledgeSum(Sites) As Integer 'total number of fledglings in one year

Dim RecruitersSum(Sites) As Integer 'Number of juveniles moving into the floating group in a year

Dim ExitFloating(Sites) As Integer 'Number of adults leaving the floating category in a year

AdultsFloating(Sites) As Integer 'Number of adults entering floating from a territory

Dim DiesWhileFloating(Sites) As Integer 'Number of birds dying whilst in the floating category



```

Dim TotalAdults(Sites) As Integer      'Number of adults in floating and on territory
Dim AdultsDying(Sites) As Integer      'Adults dying in one year, inc those dying whilst floating
Dim BreedingAdults(Sites) As Integer  'Number of adults on territory
Dim AgeRecruitment(1000, Sites) As Integer : Dim MeanAgeRecruitment As Single : Dim SumAgeR As Integer 'estimating mean age at recruitment
Dim TotalRecruited(Sites) As Integer
Dim OJuv(Sites) As Integer: OJuv(1) = 28 'dwp number of juvenile present in a site at mid winter, start of model
OJuv(2) = 6 : OJuv(3) = 4 : OJuv(4) = 10 'bb, mh, 'pb
Dim HabSite As Integer 'site where habitat improvement is taking place
Dim cJuv(Sites) As Integer 'for site removal sim -5, when starting population and thus starting number of juveniles varies
Dim Effort As Integer : Dim Pred_C(Sites) As Integer 'level of predator control at a site
Dim P_chicks(4) As Single 'increase the Daily Brood Survival for predator control simulation
Dim P_nests(4, 4) As Single 'increase Daily Nest Survival for the cat reduction simulations
Select Case simulation_number
    Case Is = 6, 10, 5
        P_chicks(1) = 0 'site specific sim - 6, half effect size specified in paper, as each real site is half a model site
        P_chicks(2) = 0.00180625 : P_chicks(3) = 0.0036125
        P_nests(1, 1) = 0 : P_nests(1, 2) = 0.1150249 : P_nests(1, 3) = 0.2101015 'dwp, baseline, 25% cat control, 50% cat control
        P_nests(2, 1) = 0 : P_nests(2, 2) = 0.2005194 : P_nests(2, 3) = 0.2968091 'bb
        P_nests(3, 1) = 0 : P_nests(3, 2) = 0.3397645 : P_nests(3, 3) = 0.4400525 'mh
        P_nests(4, 1) = 0 : P_nests(4, 2) = 0.2500374 : P_nests(4, 3) = 0.3479361 'pb
    End Select

Dim Stay(4, 4) As Single 'chance that juvenile birds stay in natal site, index of qual (DispOption5)
Stay(1, 1) = 0.5148551 : Stay(1, 2) = 0.2186542 : Stay(1, 3) = 0.0537664 : Stay(1, 4) = 0.1236036
Select Case simulation_number
    Case Is = 6, 10, 5
        Stay(1, 1) = 0.5148551 : Stay(1, 2) = 0.2186542 : Stay(1, 3) = 0.0537664 : Stay(1, 4) = 0.1236036 'baseline
        Stay(2, 1) = 0.55478723 : Stay(2, 2) = 0.244401 : Stay(2, 3) = 0.06784983 : Stay(2, 4) = 0.14505429 '25% cat reduction
        Stay(3, 1) = 0.59770555 : Stay(3, 2) = 0.27306711 : Stay(3, 3) = 0.08546907 : Stay(3, 4) = 0.1700831 '50% cat reduction
    End Select

Dim SiteCounter As Integer = 1 : Dim SiteSection As Integer = 0
Dim RecruitSite(Sites, Sites) As Integer 'Where do the juveniles recruit ?
Dim SS As Single = 0.5 'For starting population size sim - 3, multiplier of starting population size for each sim
Dim cAdult As Double 'Correction for Adult survival in demographic sensitivity, sim - 11

```

```

Dim NestBeta(Sites) As Single 'survival parameters for that year
Dim ChickSurvivalAll(Sites) As Single : Dim JuvenileSurvivalAll(Sites) As Single : Dim AdultSurvivalAll(Sites) As Single

'Storage vector the starting survival estimates so that they can be returned to at the start of each rep
Dim StartingNestBeta(Sites) As Single: Dim StartingZ(2) As Single: Dim StartingJuvenileSurvivalAll(2) As Single
    StartingChickSurvivalAll As Single
Dim

'Breeding parameters
Dim IncubationPeriod = 27 'average incubation period, with laying period it makes up nesting period
Dim NestingPeriod(Territory, Sites) As Integer 'length of a particular nesting attempt, with a space available for a different value for each territory
Dim DaysToFledging(Territory, Sites) As Integer 'number of days to fledging for a particular brood
Dim FledgingPeriod = 35 'average fledging period
Dim clutch(Territory, Sites) As Integer 'stores the clutch size for that breeding attempt
Const Clutch1 As Single = 0.1117647 'likelihood of 1 egg clutch
Const ChanceOfOneChickBrood As Single = 9 / 60 'likelihood of egg adding or partial predation meaning that a two egg nest hatches only one egg
Dim BroodSizeHatchingAll(Territory, Sites) As Integer
Dim ChickAge(Territory, Sites) As Integer 'stores the age of the chicks of that brood
Dim BSFledgingAll(Territory, Sites) As Integer 'size of brood at fledging, determined by TwoFledge
Dim TwoFledge As Single = 9 / 18 'the probability that two chicks fledge from a two chicks brood
Dim Handicap(Territory, Sites) As Single 'this reduces the brood survival for one parent broods
Dim JuvenileAge(1000, Sites) As Integer 'stores the age of a particular family of juveniles
Dim Juveniles(Sites) As Integer 'number of juveniles at the point of summary
Dim IFledge(Sites) As Single

Const reps = 100 'number of iterations to perform for each set of starting conditions
Dim Jday As Integer: Dim Week As Integer: Dim DofWeek As Integer: Dim Year As Integer: Dim Day As Integer 'vectors for counting time
Dim a As Single: Dim D As Single: Dim B As Single: Dim E As Single: Dim p As Single: Dim F As Single: Dim h As Single: Dim P1 As Single
    P2 As Single: Dim S As Single: Dim Z As Single: Dim DNS As Single: Dim C As Single: Dim age As Integer : Dim target As Integer = 0
Dim

FileOpen(1, "C:\Wirebird\SimulationsFinal1\dwp10.txt", OpenMode.Output) 'open a storage file for each site and print the headings
FileOpen(2, "C:\Wirebird\SimulationsFinal1\bb10.txt", OpenMode.Output): FileOpen(3, "C:\Wirebird\SimulationsFinal1\mh10.txt", OpenMode.Output)
FileOpen(4, "C:\Wirebird\SimulationsFinal1\pb10.txt", OpenMode.Output)
For site = 1 To Sites
    PrintLine(site, "Year" & "," & "boot" & "," & "Simulation" & "," & "NestBeta" & "," & "ChickSurvivalAll" & "," & "AdultSurvivalAll" & "," & "cAdult" & "," &
"JuvenileSurvivalAll" & "," & "Territories" & "," & "SumStatus(1)" & "," & "SumStatus(2)" & "," & "SumStatus(3)" & "," & "SumStatus(4)" & "," & "Occupied" & "," &
"NestSum" & "," & "BroodSum" & "," & "ChickSum" & "," & "FledgedSum" & "," & "RecruitersSum" & "," & "SumSuccessfulBroods" & "," & "TotalAdults" & "," &

```

```
"BreedingAdults" & "," & "DiesWhileFloating" & "," & "AdultsFloating" & "," & "ExitFloating" & "," & "AdultsDying" & "," & "Floating" & "," & "Juveniles" & "," &
"MAgeRecruitment" & "," & "IncubationPeriod" & "," & "FledgingPeriod" & "," & "TwoFledge" & "," & "NestInitiationWeek_V" & "," & "RecruitSite(1)" & "," &
"RecruitSite(2)" & "," & "RecruitSite(3)" & "," & "RecruitSite(4)" & "," & "Pred_C" & "," & "Dispersal")
```

```
Next site
```

```
'set up starting conditions
```

```
For sim = 1 To Simulations
```

```
For site = 1 To Sites
```

```
startTerr(site) = OstartTerr(site) : Territories(site) = OTerritories(site)
```

```
Next sim
```

```
Select Case simulation_number
```

```
Case Is = 1, 8
```

```
Dispersal = 5
```

```
Case Is = 2 'for error sensitivity analysis, each simulation select randomly from uniform distribution of each variable
```

```
IncubationPeriod = rand.Next(26, 31) 'select random integer between 26 and 30
```

```
FledgingPeriod = rand.Next(35, 38)
```

```
TwoFledge = rand.Next(7, 13) / 18
```

```
NestInitiationWeek_V = (((Nest_average + (2 * Nest_se)) - (Nest_average - (2 * Nest_se))) * Rnd() + (Nest_average - (2 * Nest_se)))
```

```
Dispersal = rand.Next(4, 7)
```

```
Case Is = 11 ' Demographic sensitivity analysis,
```

```
Dispersal = rand.Next(4, 7) 'DispOption randomly selected between 4 and 6
```

```
Territory = OTerritory + 100 'increasing K at all sites to see influence of changing demography
```

```
For i = 1 To 4
```

```
Territories(i) = OTerritories(i) + 100
```

```
Next i
```

```
Case Is = 3 'for starting population size simulation
```

```
If sim = 1 Then Dispersal = 4
```

```
For site = 1 To Sites
```

```
Territory = OTerritory * SS 'change starting number of territories
```

```
startTerr(site) = Int(OstartTerr(site) * SS) : Territories(site) = Int(OTerritories(site) * SS)
```

```
cJuv(site) = Int(OJuv(site) * SS) 'define starting number of juveniles for each starting population size
```

```
For i = 1 To cJuv(site) 'define the age of each juvenile
```

```

        JuvenileAll(i, site) = 1 : JuvenileAge(i, site) = rand.Next(204, 455)
    Next i
Next site
Territory = Int(OTerritory * SS)

Case Is = 5 'site removal, remove half of target site as each real site is half of a model site
ZeroSite = sim - SiteSection 'defines which site is the target of removal in each simulation
If sim = 1 Then Dispersal = 4
Territories(ZeroSite) = Territories(ZeroSite) / 2
E = startTerr(ZeroSite) / 2
For i = OJuv(ZeroSite) + 1 To E + OJuv(ZeroSite) + 1
    JuvenileAll(i, ZeroSite) = 1 : JuvenileAge(i, ZeroSite) = 455
Next i
startTerr(ZeroSite) = startTerr(ZeroSite) / 2
Select Case sim 'extra territories for remaining sites
    Case Is > 24
        For i = 1 To Sites
            Territory = OTerritory + 50
            If i <> ZeroSite Then Territories(i) = Territories(i) + 50
        Next i
    End Select
If sim > 12 And sim < 37 Then Effort = 1 Else Effort = 0 'predator control for the remaining sites
For i = 1 To 4
    Pred_C(i) = Effort
    If Effort = 1 Then IFledge(i) = 0.0625 : If Effort = 2 Then IFledge(i) = 0.125 'increase proportion of chicks that fledge from a brood
Next i

Case Is = 6 'for predator control simulation
ReDim Pred_C(Sites)
If sim = 1 Then Dispersal = 4 : If sim < 4 Then Effort = 0 : If sim >= 4 And sim < 16 Then Effort = 1 'for doing site specific simulations
If sim > 15 Then Effort = 2
Pred_C(target) = Effort : If Effort = 1 Then IFledge(target) = 0.03125 : If Effort = 2 Then IFledge(target) = 0.0625

Case Is = 10 'predator control and habitat improvement
If sim = 1 Then Dispersal = 4
If sim > 3 And sim < 7 Then 'habitat improvement

```

```

Territory = OTerritory + 50
For i = 1 To 4
    Territories(i) = OTerritories(i) + 50
Next i
End If
If sim > 6 And sim < 10 Then Effort = 2 'predator control
If sim > 9 Then 'predator control and habitat improvement
    Territory = OTerritory + 50 : Effort = 2
    For i = 1 To 4
        Territories(i) = OTerritories(i) + 50
    Next i
End If
For i = 1 To 4 'equal predator control at all sites
    Pred_C(i) = Effort : If Effort = 1 Then IFledge(i) = 0.0625 : If Effort = 2 Then IFledge(i) = 0.125
Next i
End Select

'STARTING CONDITIONS
Select Case simulation_number 'Nest Survival
Case Is = 1 'overall estimate, random selection from normal cumulative distribution
    For site = 1 To Sites
        a = Rnd() : If site = 1 Then StartingNestBeta(1) = oExcel.WorksheetFunction.NormInv(a, Beta1, SEMeanNestBeta) - Beta1
        If site > 1 Then StartingNestBeta(site) = oExcel.WorksheetFunction.NormInv(a, MeanNestBeta(site - 1), SEMeanNestBeta)
    Next site
Case Is = 11 'sensitivity analysis, random selection from uniform distribution
    Nest_correct = 4 * SEMeanNestBeta * Rnd() - (2 * SEMeanNestBeta)
    For site = 1 To Sites
        If site = 1 Then
            StartingNestBeta(1) = Nest_correct
        Else : StartingNestBeta(site) = MeanNestBeta(site - 1) + Nest_correct
        End If
    Next site
Case Is = 6, 7, 10, 5 'when an increase in nest survival from predator control is simulated
    For site = 1 To Sites
        If site = 1 Then StartingNestBeta(site) = 0 + P_nests(site, Pred_C(site) + 1)
        If site > 1 Then StartingNestBeta(site) = MeanNestBeta(site - 1) + P_nests(site, Pred_C(site) + 1)
    Next site

```

```

Next site
Case Else 'others, using mean value only
For site = 1 To Sites
    If site = 1 Then StartingNestBeta(site) = 0 : If site > 1 Then StartingNestBeta(site) = MeanNestBeta(site - 1)
Next site
End Select

Select Case simulation_number 'Adult and juvenile survival, options as for nest survival
Case Is = 1
    For i = 1 To 2
        C = Rnd() : StartingZ(i) = oExcel.WorksheetFunction.NormInv(C, MeanDailyAdultSurvivalAll(i), SEDailyAdultSurvivalAll)
        D = Rnd()
        StartingJuvenileSurvivalAll(i) = oExcel.WorksheetFunction.NormInv(D, MeanDailyJuvenileSurvivalAll(i), SEDailyJuvenileSurvivalAll)
    Next i
Case Is = 11
    cAdult = ((2 * SEDailyAdultSurvivalAll) - (-2 * SEDailyAdultSurvivalAll)) * Rnd() - 2 * SEDailyAdultSurvivalAll
    E = ((2 * SEDailyJuvenileSurvivalAll) - (-2 * SEDailyJuvenileSurvivalAll)) * Rnd() - 2 * SEDailyJuvenileSurvivalAll
    For i = 1 To 2
        StartingZ(i) = MeanDailyAdultSurvivalAll(i) + cAdult
        StartingJuvenileSurvivalAll(i) = MeanDailyJuvenileSurvivalAll(i) + E
    Next i
Case Is = 6, 7
    For i = 1 To 2
        If ASAll = 1 Then
            StartingZ(i) = MeanDailyAdultSurvivalAll(1) : StartingJuvenileSurvivalAll(i) = MeanDailyJuvenileSurvivalAll(i)
        Else : StartingZ(i) = MeanDailyAdultSurvivalAll(i) : StartingJuvenileSurvivalAll(i) = MeanDailyJuvenileSurvivalAll(i)
        End If
    Next i
Case Else
    For i = 1 To 2
        StartingZ(i) = MeanDailyAdultSurvivalAll(i) : StartingJuvenileSurvivalAll(i) = MeanDailyJuvenileSurvivalAll(i)
    Next i
End Select

B = Rnd()
Select Case simulation_number 'Brood survival, options as for nest survival

```

```

Case Is = 1
    StartingChickSurvivalAll = oExcel.WorksheetFunction.NormInv(B, MeanDailyChickSurvivalAll, SEMeanDailyChickSurvivalAll)
Case Is = 11
    StartingChickSurvivalAll = (MeanDailyChickSurvivalAll + (2 * SEMeanDailyChickSurvivalAll) - (MeanDailyChickSurvivalAll - (2 *
SEMeanDailyChickSurvivalAll))) * Rnd() + (MeanDailyChickSurvivalAll - (2 * SEMeanDailyChickSurvivalAll))
Case Else
    StartingChickSurvivalAll = MeanDailyChickSurvivalAll
End Select

Dim start As Single : start = Microsoft.VisualBasic.DateAndTime.Timer

For boot = 1 To reps 'start replication number one
    Console.WriteLine("New Rep: " & Microsoft.VisualBasic.DateAndTime.Timer - start)
    start = Microsoft.VisualBasic.DateAndTime.Timer
    If simulation_number = 1 Then Dispersal = rand.Next(4, 7) 'dispersal is randomly varied between options 4,5,6 for simulation number 1

    'after one rep all these variables must be returned to their default states, which is mostly zero
    ReDim StatusAll(Territory, Sites): ReDim JuvenileAll(1000, Sites): ReDim Floating(Sites):
    ProbNestInitiationAll = 0: ReDim NestingPeriod(Territory, Sites): ReDim DaysToFledging(Territory, Sites):
    ReDim clutch(Territory, Sites): ReDim ChickAge(Territory, Sites): ReDim BroodSizeHatchingAll(Territory, Sites):
    ReDim BSFledgingAll(Territory, Sites): ReDim NestSum(Sites): ReDim BroodSum(Sites):
    ReDim ChickSum(Sites): ReDim FledgeSum(Sites): ReDim DiesWhileFloating(Sites):
    ReDim RecruitorsSum(Sites): ReDim AdultsFloating(Sites): ReDim ExitFloating(Sites):
    ReDim TotalAdults(Sites): ReDim AdultsDying(Sites): ReDim BreedingAdults(Sites):
    ReDim SumSuccessfulBroods(Sites): ReDim Handicap(Territory, Sites): ReDim JuvenileAge(1000, Sites):
    ReDim SumStatus(4, Sites): ReDim Juveniles(Sites): ReDim AgeRecruitment(1000, Sites):
    ReDim TotalRecruited(Sites): ReDim RecruitSite(Sites, Sites)

    'return all the survival values to the starting conditions for the simulation at the start of a new rep
    For site = 1 To Sites
        NestBeta(site) = StartingNestBeta(site)
        If site = 1 Or site = 2 Or site = 4 Then AdultSurvivalAll(site) = ((Math.Sin(StartingZ(1)) + 1) / 2) ^ (12 / 365) Else AdultSurvivalAll(site) =
        ((Math.Sin(StartingZ(2)) + 1) / 2) ^ (12 / 365)
        If site = 1 Then JuvenileSurvivalAll(site) = StartingJuvenileSurvivalAll(1) Else JuvenileSurvivalAll(site) = StartingJuvenileSurvivalAll(2)
        ChickSurvivalAll(site) = StartingChickSurvivalAll + P_chicks(Pred_C(site) + 1)
        For i = 1 To OJuv(site)

```

```

    JuvenileAll(i, site) = 1 : JuvenileAge(i, site) = rand.Next(204, 455)
Next i
Next site

```

Select Case simulation\_number 'site removal, make sure correct number of territories after redims

```

Case Is = 5
    startTerr(ZeroSite) = OstartTerr(ZeroSite) : E = startTerr(ZeroSite) / 2
    For i = OJuv(ZeroSite) + 1 To E + OJuv(ZeroSite) + 1
        JuvenileAll(i, ZeroSite) = 1 : JuvenileAge(i, ZeroSite) = 455
    Next i
    startTerr(ZeroSite) = startTerr(ZeroSite) / 2
End Select

```

For site = 1 To Sites 'loop to determine starting states of each territory

```

    For Terr = 1 To startTerr(site)
        StatusAll(Terr, site) = 2 : SumStatus(3, site) = SumStatus(3, site) + 1 : Handicap(Terr, site) = 1 'Default handicap = 1, this has no effect
    Next Terr
    For Terr = (startTerr(site) + 1) To Territories(site)
        StatusAll(Terr, site) = 0 : SumStatus(1, site) = SumStatus(1, site) + 1 : Handicap(Terr, site) = 1
    Next Terr
    Occupied(site) = SumStatus(2, site) + SumStatus(3, site) + SumStatus(4, site)
    FreeT = SumStatus(1, 1) + SumStatus(1, 2) + SumStatus(1, 3) + SumStatus(1, 4)
    BreedingAdults(site) = SumStatus(2, site) + 2 * (SumStatus(3, site) + SumStatus(4, site))
    TotalAdults(site) = Floating(site) + BreedingAdults(site)
Next site

```

For site = 1 To Sites 'Print the starting conditions

```

    PrintLine((site), "0" & " " & boot & " " & sim & " " & NestBeta(site) & " " & ChickSurvivalAll(site) & " " & AdultSurvivalAll(site) & " " & cAdult & " " &
    JuvenileSurvivalAll(site) & " " & Territories(site) & " " & SumStatus(1, site) & " " & SumStatus(2, site) & " " & SumStatus(3, site) & " " & SumStatus(4, site) & " " &
    Occupied(site) & " " & "0" & " " & "0" & " " & "0" & " " & "0" & " " & "0" & " " & "0" & " " & TotalAdults(site) & " " & BreedingAdults(site) & " " & "0" & " " & "0" &
    " " & "0" & " " & "0" & " " & "0" & " " & "0" & " " & "0" & " " & IncubationPeriod & " " & FledgingPeriod & " " & TwoFledge & " " & NestInitiationWeek_V & " " &
    RecruitSite(site, 1) & " " & RecruitSite(site, 2) & " " & RecruitSite(site, 3) & " " & RecruitSite(site, 4) & " " & Pred_C(site) & " " & Dispersal)
Next site

```

'start the main part of the model

```

Jday = 183 : Week = 27 : DofWeek = 1 : Year = 0

```



```

For Day = 1 To (Duration * 365) 'starting day loop
  For site = 1 To Sites

    'For the Floating Group, if there are any non-territorial birds do they survive today?
    Select Case Floating(site)
      Case Is > 0
        For Float = 1 To Floating(site)
          E = Rnd()
          If E > AdultSurvivalAll(site) Then Floating(site) = Floating(site) - 1 : DiesWhileFloating(site) = DiesWhileFloating(site) + 1 'bird dies'
        Next Float
      End Select

    'For empty Territories 'Are there enough birds in the floating popuation to make a pair? depending on floating pop size gives the likelihood of
    there being a male and a female. If this is not met then don't try again. If one pair moves in then see if floating is still above 2 and then try again.
    For Terr = 1 To Territories(site)
      If Floating(site) < 2 Then Exit For 'Exit loop if there are fewer than 2 birds in floating
      If SumStatus(1, site) = 0 Then Exit For 'Exit loop if there are no empty territories
      Select Case StatusAll(Terr, site)
        Case 0
          Select Case Floating(site)
            Case Is < 10
              p = Rnd()
              If p > ChanceOfAPair(Floating(site)) Then
                Floating(site) = Floating(site) - 2 : StatusAll(Terr, site) = 2 : ExitFloating(site) = ExitFloating(site) + 2
              Else
                Exit For
              End If
            Case Else
              Floating(site) = Floating(site) - 2 : StatusAll(Terr, site) = 2 : ExitFloating(site) = ExitFloating(site) + 2
            End Select
          End Select
        End Select
      Next Terr

    'For the territorial pairs that are not currently breeding
    SumStatus(1, site) = 0 : SumStatus(2, site) = 0 : SumStatus(3, site) = 0 : SumStatus(4, site) = 0 'Update in case any new territories are full
    For Terr = 1 To Territories(site)

```

```

    If StatusAll(Terr, site) = 0 Then SumStatus(1, site) = SumStatus(1, site) + 1
    If StatusAll(Terr, site) = 1 Then SumStatus(2, site) = SumStatus(2, site) + 1
    If StatusAll(Terr, site) = 2 Then SumStatus(3, site) = SumStatus(3, site) + 1
    If StatusAll(Terr, site) = 3 Then SumStatus(4, site) = SumStatus(4, site) + 1
    If StatusAll(Terr, site) > 3 Then Debug.Print("Error status is greater than 3")
Next Terr
Occupied(site) = SumStatus(2, site) + SumStatus(3, site) + SumStatus(4, site)
FreeT = SumStatus(1, 1) + SumStatus(1, 2) + SumStatus(1, 3) + SumStatus(1, 4)

For Terr = 1 To Territories(site)
    If SumStatus(3, site) = 0 Then Exit For
    If Occupied(site) = 0 Then Debug.Print("Error occupied zero and sumstatus 3 greater than zero")
    If StatusAll(Terr, site) <> 2 Then GoTo LastLine

    For bird = 1 To 2 'Do they survive today?
        F = Rnd() : If F > AdultSurvivalAll(site) Then StatusAll(Terr, site) = StatusAll(Terr, site) - 1 : AdultsDying(site) = AdultsDying(site) + 1
    Next bird
    If StatusAll(Terr, site) = 1 Then StatusAll(Terr, site) = 0 : Floating(site) = Floating(site) + 1 : AdultsFloating(site) = AdultsFloating(site) + 1 'if
    one bird left, territory empties and bird enters floating
    If StatusAll(Terr, site) <> 2 Then GoTo LastLine 'If both birds die territory empties
    If SumStatus(3, site) < 1 Then Debug.Print("no non-breeding territories but in nest initiation routine")

    'Does the territory start a nest today?
    'NestInitiationWeek corrected for the number of pairs that could start a nest that day (# of occupied T/#of non breeding T)
    ProbNestInitiationAll = ((Occupied(site) / SumStatus(3, site)) * NestInitiationWeek(Week)) * detection(site)
    Select Case simulation_number
        Case Is = 2
            ProbNestInitiationAll = ProbNestInitiationAll * (NestInitiationWeek_V / Nest_average) 'for error sense simulation
    End Select
    p = Rnd() : If p < ProbNestInitiationAll Then StatusAll(Terr, site) = 3 : NestSum(site) = NestSum(site) + 1 'a nest is initiated
    Select Case StatusAll(Terr, site) 'If a nest starts, define clutch size & nesting period, these nests go into the breeding loop today
        Case 3
            p = Rnd() : If p < Clutch1 Then clutch(Terr, site) = 1 : If p >= Clutch1 Then clutch(Terr, site) = 2
            If clutch(Terr, site) < 1 Or clutch(Terr, site) > 2 Then Debug.Print("specifying clutch size is not working")
            NestingPeriod(Terr, site) = IncubationPeriod + clutch(Terr, site)
    End Select

```

LastLine:        Next Terr

'for those territories already breeding, do the adults survive today?

For Terr = 1 To Territories(site)

  If StatusAll(Terr, site) = 2 Or StatusAll(Terr, site) = 0 Then GoTo LastLine3 'get rid of non-breeding territories

  Select Case NestingPeriod(Terr, site) 'don't ask the ones that have just initiated a nest whether they die as they have been asked already

    Case Is < 28

      Select Case StatusAll(Terr, site)

        Case 1 'single parent bird

          h = Rnd() : If h > AdultSurvivalAll(site) Then StatusAll(Terr, site) = 0 : AdultsDying(site) = AdultsDying(site) + 1 \_  
          : BroodSizeHatchingAll(Terr, site) = 0 : DaysToFledging(Terr, site) = 0 : ChickAge(Terr, site) = 0 : Handicap(Terr, site) = 1

        Case 3 'two parent birds

          P1 = Rnd() : P2 = Rnd()

          If P1 > AdultSurvivalAll(site) Or P2 > AdultSurvivalAll(site) Then StatusAll(Terr, site) = 1 'if one adult dies, status changes to 1

          If P1 > AdultSurvivalAll(site) And P2 > AdultSurvivalAll(site) And BroodSizeHatchingAll(Terr, site) > 0 Then StatusAll(Terr, site) = 0 \_  
          : AdultsDying(site) = AdultsDying(site) + 2 : BroodSizeHatchingAll(Terr, site) = 0 : DaysToFledging(Terr, site) = 0 :

          ChickAge(Terr, site) = 0 'if two adults die the territory empties

          If P1 > AdultSurvivalAll(site) And P2 > AdultSurvivalAll(site) And NestingPeriod(Terr, site) > 0 Then NestingPeriod(Terr, site) = 0  
          : StatusAll(Terr, site) = 0 \_ : AdultsDying(site) = AdultsDying(site) + 2 'If the nest/brood fails zero the breeding components

          If StatusAll(Terr, site) = 1 And NestingPeriod(Terr, site) > 0 Then StatusAll(Terr, site) = 0 : AdultsDying(site) = AdultsDying(site) + 1  
          : Floating(site) = Floating(site) + 1 : AdultsFloating(site) = AdultsFloating(site) + 1 : NestingPeriod(Terr, site) = 0 'If one adult dies at nesting stage breeding attempt fails

          If StatusAll(Terr, site) = 1 And BroodSizeHatchingAll(Terr, site) > 0 Then Handicap(Terr, site) = 2 : AdultsDying(site) = AdultsDying(site) + 1  
          'If one adult dies at brood stage daily chick survival is reduced by half

      End Select

  Case Is = 28 'for parent birds with 2eggs this is day2 and they should enter survival loop, for 1egg clutches it is day1 and they should not

    Select Case clutch(Terr, site)

      Case Is = 2

        P1 = Rnd() : P2 = Rnd()

        If P1 > AdultSurvivalAll(site) Or P2 > AdultSurvivalAll(site) Then StatusAll(Terr, site) = 1 'if one adult dies, then status changes to 1

        If P1 > AdultSurvivalAll(site) And P2 > AdultSurvivalAll(site) And BroodSizeHatchingAll(Terr, site) > 0 Then StatusAll(Terr, site) = 0 \_  
        : AdultsDying(site) = AdultsDying(site) + 2 : BroodSizeHatchingAll(Terr, site) = 0 : DaysToFledging(Terr, site) = 0 :

        ChickAge(Terr, site) = 0 'if two adults die the territory empties

        If P1 > AdultSurvivalAll(site) And P2 > AdultSurvivalAll(site) And NestingPeriod(Terr, site) > 0 Then NestingPeriod(Terr, site) = 0  
        : StatusAll(Terr, site) = 0 \_ : AdultsDying(site) = AdultsDying(site) + 2

```

    If StatusAll(Terr, site) = 1 And NestingPeriod(Terr, site) > 0 Then StatusAll(Terr, site) = 0 : AdultsDying(site) = AdultsDying(site) +
    1 : Floating(site) = Floating(site) + 1 : AdultsFloating(site) = AdultsFloating(site) + 1 : NestingPeriod(Terr, site) = 0 'If one adult dies
    at nesting stage breeding attempt fails
    If StatusAll(Terr, site) = 1 And BroodSizeHatchingAll(Terr, site) > 0 Then Handicap(Terr, site) = 2 : AdultsDying(site) =
    AdultsDying(site) + 1 'If one adult dies at brood stage daily chick survival is reduced by half
End Select
End Select
If StatusAll(Terr, site) = 0 Then GoTo LastLine3

'Breeding - Does the nest survive today?
Select Case NestingPeriod(Terr, site)
Case Is > 0
    If Jday > 0 And Jday < 100 Then NestDay = Jday + 60 'converting the day of the year to the day of the field season to get DNS estimate
    If Jday >= 100 And Jday < 305 Then NestDay = 58 'if during winter then use average value (mid season)
    If Jday >= 305 Then NestDay = Jday - 304
    p = Rnd() 'backtransform from beta values
    DNS = Math.Exp(Beta1 + (Nest(1, site) * NestBeta(1)) + (Nest(2, site) * NestBeta(2)) + (Nest(3, site) * NestBeta(3)) + (Nest(4, site) *
    NestBeta(4)) + (NestBDate * NestDay) + (NestBAge * ((IncubationPeriod + clutch(Terr, site) + 1) - NestingPeriod(Terr, site)))) / _
    (1 + Math.Exp(Beta1 + (Nest(1, site) * NestBeta(1)) + (Nest(2, site) * NestBeta(2)) + (Nest(3, site) * NestBeta(3)) + (Nest(4, site) *
    NestBeta(4)) + (NestBDate * NestDay) + (NestBAge * ((IncubationPeriod + clutch(Terr, site) + 1) - NestingPeriod(Terr, site))))))
    If p > DNS Then StatusAll(Terr, site) = 2 : NestingPeriod(Terr, site) = 0 'nest fails
    If StatusAll(Terr, site) = 2 Then GoTo LastLine3
    NestingPeriod(Terr, site) = NestingPeriod(Terr, site) - 1 'If survives gets one day closer to hatching

'Does the nest hatch today?
Select Case NestingPeriod(Terr, site)
Case 0
    BroodSizeHatchingAll(Terr, site) = 0 'only those with nest not chicks selected
    Select Case clutch(Terr, site)
    Case 1
        BroodSizeHatchingAll(Terr, site) = 1 : DaysToFledging(Terr, site) = FledgingPeriod : ChickAge(Terr, site) = 0 :
        BroodSum(site) = BroodSum(site) + 1 : ChickSum(site) = ChickSum(site) + 1
    Case Else
        P1 = Rnd() 'determining proportion of clutch that hatches
        If P1 > ChanceOfOneChickBrood Then BroodSizeHatchingAll(Terr, site) = 2 : DaysToFledging(Terr, site) = FledgingPeriod :
        ChickAge(Terr, site) = 0 : BroodSum(site) = BroodSum(site) + 1 : ChickSum(site) = ChickSum(site) + 2
    End Select
End Select

```

```

        If P1 <= ChanceOfOneChickBrood Then BroodSizeHatchingAll(Terr, site) = 1 : DaysToFledging(Terr, site) = FledgingPeriod :
            ChickAge(Terr, site) = 0 : BroodSum(site) = BroodSum(site) + 1 : ChickSum(site) = ChickSum(site) + 1
        End Select
    If DaysToFledging(Terr, site) = 35 Then GoTo LastLine3
End Select
End Select

```

'those pairs that have one or two chicks enter the brood area the day after they hatch

```

Select Case BroodSizeHatchingAll(Terr, site)
Case Is > 0
    If DaysToFledging(Terr, site) < 1 Then Debug.Print("DaysToFledging <1 in the brood loop")
    If StatusAll(Terr, site) = 0 Or StatusAll(Terr, site) = 2 Then Debug.Print("Non-breeders are in the brood loop")
    P1 = Rnd(): If P1 > ChickSurvivalAll(site) / Handicap(Terr, site) Then BroodSizeHatchingAll(Terr, site) = 0 'chicks die
    If BroodSizeHatchingAll(Terr, site) = 0 And StatusAll(Terr, site) = 1 Then StatusAll(Terr, site) = 0 : Floating(site) = Floating(site) + 1 :
        AdultsFloating(site) = AdultsFloating(site) + 1 : ChickAge(Terr, site) = 0 : DaysToFledging(Terr, site) = 0 : Handicap(Terr, site) = 1
    If BroodSizeHatchingAll(Terr, site) = 0 And StatusAll(Terr, site) = 3 Then StatusAll(Terr, site) = 2 : DaysToFledging(Terr, site) = 0 :
        ChickAge(Terr, site) = 0 'if chicks die a single parent enters floating pop and mated parents enter non-breeding group.
    If BroodSizeHatchingAll(Terr, site) = 0 Then GoTo LastLine3
    DaysToFledging(Terr, site) = DaysToFledging(Terr, site) - 1 : ChickAge(Terr, site) = ChickAge(Terr, site) + 1

```

'Do the chicks fledge today?

```

Select Case DaysToFledging(Terr, site)
Case 0
    If StatusAll(Terr, site) = 1 Then StatusAll(Terr, site) = 0 : Floating(site) = Floating(site) + 1 : AdultsFloating(site) =
        AdultsFloating(site) + 1 : ChickAge(Terr, site) = 0 : Handicap(Terr, site) = 1 : BroodSizeHatchingAll(Terr, site) = 0
    If StatusAll(Terr, site) = 3 Then StatusAll(Terr, site) = 2 : ChickAge(Terr, site) = 0 : BroodSizeHatchingAll(Terr, site) = 0
    SumSuccessfulBroods(site) = SumSuccessfulBroods(site) + 1 'Counts the number of successful broods
    P1 = Rnd() : If P1 <= TwoFledge + IFledge(site) Then BSFledgingAll(Terr, site) = 1 'defines number of fledglings in the successful brood
    If P1 > TwoFledge + IFledge(site) Then BSFledgingAll(Terr, site) = 1 'defines number of fledglings in the successful brood
    If BSFledgingAll(Terr, site) < 1 Or BSFledgingAll(Terr, site) > 2 Then Debug.Print("BSFledging is not working properly")
    FledgeSum(site) = FledgeSum(site) + BSFledgingAll(Terr, site) 'Counts the number of fledglings
    For i = 1 To 1000 'fit the fledglings into the next empty pot
        If JuvenileAll(i, site) = 0 Then JuvenileAll(i, site) = BSFledgingAll(Terr, site) : JuvenileAge(i, site) = 66 : BSFledgingAll(Terr,
            site) = 0
        If BSFledgingAll(Terr, site) = 0 Then Exit For
    Next i

```

```

        End Select
    End Select
LastLine3:    Next Terr

'Juvenile loop
For i = 1 To 1000
    Select Case JuvenileAll(i, site) 'do the juveniles survive today?
        Case Is > 0
            For juv = 1 To JuvenileAll(i, site)
                p = Rnd() : If p > JuvenileSurvivalAll(site) Then JuvenileAll(i, site) = JuvenileAll(i, site) - 1 'one bird dies
                If JuvenileAll(i, site) = 0 Then GoTo LastLineJ
            Next juv
            JuvenileAge(i, site) = JuvenileAge(i, site) + 1

            For juv = 1 To JuvenileAll(i, site) 'do they move into the floating population
                Select Case JuvenileAge(i, site)
                    Case 204 To 454
                        p = Rnd() : If p < Recruitment(JuvenileAge(i, site)) Then JuvenileAll(i, site) = JuvenileAll(i, site) - 1 : Recruited = 1 : age = 1
                        For j = 1 To 1000 'store age at recruitment
                            If Recruited = 0 Then Exit For
                            If AgeRecruitment(j, site) = 0 Then AgeRecruitment(j, site) = JuvenileAge(i, site) : age = 0
                            If age = 0 Then Exit For
                        Next j
                    Case Is > 454
                        JuvenileAll(i, site) = JuvenileAll(i, site) - 1 : Recruited = 1 : age = 1
                        For j = 1 To 1000 'store age at recruitment
                            If Recruited = 0 Then Exit For
                            If AgeRecruitment(j, site) = 0 Then AgeRecruitment(j, site) = JuvenileAge(i, site) : age = 0
                            If age = 0 Then Exit For
                        Next j
                End Select
            End Select
            Select Case Recruited
                Case Is = 1 'If a bird has just recruited determine which site they go to, depending on the dispOption for that simulation
                    Select Case Dispersal
                        Case Is = 1 'for no dispersal even when a site is full

```

```

Floating(site) = Floating(site) + 1 : RecruitorsSum(site) = RecruitorsSum(site) + 1 : Recruited = 0 : RecruitSite(site, site) =
RecruitSite(site, site) + 1
Case Is = 2 No dispersal unless a site is full, if no free territories anywhere then stay at home
Select Case FreeT
Case Is > 0
Select Case SumStatus(1, site)
Case Is > 0
Floating(site) = Floating(site) + 1 : RecruitorsSum(site) = RecruitorsSum(site) + 1 : Recruited = 0 : RecruitSite(site,
site) = RecruitSite(site, site) + 1
Case Else
Do While Recruited = 1
S = rand.Next(1, 5) 'picks a random site number between 1 and 4
If SumStatus(1, S) > 0 Then Floating(S) = Floating(S) + 1 : RecruitorsSum(site) = RecruitorsSum(site) + 1 :
Recruited = 0 : RecruitSite(site, S) = RecruitSite(site, S) + 1
Loop
End Select
Case Is = 0
Floating(site) = Floating(site) + 1 : RecruitorsSum(site) = RecruitorsSum(site) + 1 : Recruited = 0 : RecruitSite(site, site)
= RecruitSite(site, site) + 1
End Select
Case Is = 3 'random dispersal unless one is full
Select Case FreeT
Case Is > 0
Do While Recruited = 1
S = rand.Next(1, 5) 'picks a random site number between 1 and 4
If SumStatus(1, S) > 0 Then Floating(S) = Floating(S) + 1 : RecruitorsSum(site) = RecruitorsSum(site) + 1 : Recruited
= 0 : RecruitSite(site, S) = RecruitSite(site, S) + 1
Loop
Case Is = 0
Do While Recruited = 1
S = rand.Next(1, 5) 'picks a random site number between 1 and 4
Floating(S) = Floating(S) + 1 : RecruitorsSum(site) = RecruitorsSum(site) + 1 : Recruited = 0 : RecruitSite(site, S) =
RecruitSite(site, S) + 1
Loop
End Select
Case Is = 4 '50% stay in natal site and rest go elsewhere closest more frequently (0.5,0.3,0.1,0.1)

```

```

Select Case FreeT
Case Is > 0
Do While Recruited = 1
S = PartDisp1(rand.Next(1, 11), site)
If SumStatus(1, S) > 0 Then Floating(S) = Floating(S) + 1 : RecruitorsSum(site) = RecruitorsSum(site) + 1 : Recruited
= 0 : RecruitSite(site, S) = RecruitSite(site, S) + 1
Loop
Case Is = 0
Do While Recruited = 1
S = PartDisp1(rand.Next(1, 11), site)
Floating(S) = Floating(S) + 1 : RecruitorsSum(site) = RecruitorsSum(site) + 1 : Recruited = 0 : RecruitSite(site, S) =
RecruitSite(site, S) + 1
Loop
End Select
If Recruited = 1 Then Debug.Print("Something is wrong with recruitment ")
Case Is = 5 'site quality, test natal site, if good stay if not go to nearest site and repeat
Select Case FreeT
Case Is > 0
For p = 1 To 4
Z = Rnd()
If Z <= Stay(Pred_C(site + PartDisp2(p, site)) + 1, site + PartDisp2(p, site)) Then
Floating(site + (PartDisp2(p, site))) = Floating(site + (PartDisp2(p, site))) + 1
RecruitorsSum(site) = RecruitorsSum(site) + 1
Recruited = 0 : RecruitSite(site, (site + (PartDisp2(p, site)))) = RecruitSite(site, (site + (PartDisp2(p, site)))) + 1
End If
If Recruited = 0 Then Exit For
Next p
If Recruited = 1 Then
Do While Recruited = 1
S = rand.Next(1, 5)
If SumStatus(1, S) > 0 Then Floating(S) = Floating(S) + 1 : RecruitorsSum(site) = RecruitorsSum(site) + 1 :
Recruited = 0 : RecruitSite(site, S) = RecruitSite(site, S) + 1
Loop
End If
Case Is = 0
Do While Recruited = 1

```



```

        S = rand.Next(1, 5)
        Floating(S) = Floating(S) + 1 : RecruitorsSum(site) = RecruitorsSum(site) + 1 : Recruited = 0 : Recruited = 0 :
        RecruitSite(site, S) = RecruitSite(site, S) + 1
    Loop
End Select
Case Is = 6 'Go to site in proportion to number of free territories
Select Case FreeT
Case Is > 0
    For p = 1 To Sites
        PropFree(p) = SumStatus(1, p) / (SumStatus(1, 1) + SumStatus(1, 2) + SumStatus(1, 3) + SumStatus(1, 4))
    Next p
    a = Rnd()
    If a <= PropFree(1) Then Floating(1) = Floating(1) + 1 : RecruitorsSum(site) = RecruitorsSum(site) + 1 : Recruited = 0 :
    Recruited = 0 : RecruitSite(site, 1) = RecruitSite(site, 1) + 1
    If a > PropFree(1) And a <= (PropFree(2) + PropFree(1)) Then Floating(2) = Floating(2) + 1 : RecruitorsSum(site) =
    RecruitorsSum(site) + 1 : Recruited = 0 : Recruited = 0 : RecruitSite(site, 2) = RecruitSite(site, 2) + 1
    If a > PropFree(2) + PropFree(1) And a <= PropFree(1) + PropFree(2) + PropFree(3) Then Floating(3) = Floating(3) + 1 :
    RecruitorsSum(site) = RecruitorsSum(site) + 1 : Recruited = 0 : Recruited = 0 : RecruitSite(site, 3) = RecruitSite(site, 3) +
    1
    If a > PropFree(1) + PropFree(2) + PropFree(3) Then Floating(4) = Floating(4) + 1 : RecruitorsSum(site) =
    RecruitorsSum(site) + 1 : Recruited = 0 : Recruited = 0 : RecruitSite(site, 4) = RecruitSite(site, 4) + 1
Case Is = 0
    Do While Recruited = 1
        S = rand.Next(1, 5)
        Floating(S) = Floating(S) + 1 : RecruitorsSum(site) = RecruitorsSum(site) + 1 : Recruited = 0 : Recruited = 0 :
        RecruitSite(site, S) = RecruitSite(site, S) + 1
    Loop
End Select
End Select
End Select
Next juv
End Select
Next i
LastLineJ:
'create a vector of the number of territories in each state at the end of each day
SumStatus(1, site) = 0: SumStatus(2, site) = 0: SumStatus(3, site) = 0: SumStatus(4, site) = 0

```

```

For Terr = 1 To Territories(site)
  If StatusAll(Terr, site) = 0 Then SumStatus(1, site) = SumStatus(1, site) + 1
  If StatusAll(Terr, site) = 1 Then SumStatus(2, site) = SumStatus(2, site) + 1
  If StatusAll(Terr, site) = 2 Then SumStatus(3, site) = SumStatus(3, site) + 1
  If StatusAll(Terr, site) = 3 Then SumStatus(4, site) = SumStatus(4, site) + 1
  If StatusAll(Terr, site) > 3 Then Debug.Print("Error status is greater than 3")
Next Terr
Occupied(site) = SumStatus(2, site) + SumStatus(3, site) + SumStatus(4, site)
FreeT = SumStatus(1, 1) + SumStatus(1, 2) + SumStatus(1, 3) + SumStatus(1, 4)

'Output, Get the number of nests, broods, chicks and fledglings total per year and per pair per year
Select Case Jday
  Case 182
    For i = 1 To 1000
      If JuvenileAll(i, site) > 0 Then Juveniles(site) = Juveniles(site) + JuvenileAll(i, site)
    Next i

    BreedingAdults(site) = SumStatus(2, site) + 2 * (SumStatus(3, site) + SumStatus(4, site))
    TotalAdults(site) = Floating(site) + BreedingAdults(site) : AdultsDying(site) = AdultsDying(site) + DiesWhileFloating(site)
    For i = 1 To 1000
      SumAgeR = SumAgeR + AgeRecruitment(i, site)
      If AgeRecruitment(i, site) > 0 Then TotalRecruited(site) = TotalRecruited(site) + 1
    Next i
    If TotalRecruited(site) <> RecruitorsSum(site) Then Debug.Print("TRecruit <> RSum")
    MeanAgeRecruitment = SumAgeR / RecruitorsSum(site) : SumAgeR = 0

'output yearly summary to file
PrintLine((site), Year & "," & boot & "," & sim & "," & NestBeta(site) & "," _
& ChickSurvivalAll(site) & "," & AdultSurvivalAll(site) & "," & cAdult & "," & JuvenileSurvivalAll(site) & "," _
& Territories(site) & "," & SumStatus(1, site) & "," & SumStatus(2, site) & "," & SumStatus(3, site) & "," _
& SumStatus(4, site) & "," & Occupied(site) & "," & NestSum(site) & "," & BroodSum(site) & "," & ChickSum(site) & "," _
& FledgeSum(site) & "," & RecruitorsSum(site) & "," & SumSuccessfulBroods(site) & "," & TotalAdults(site) & "," _
& BreedingAdults(site) & "," & DiesWhileFloating(site) & "," & AdultsFloating(site) & "," & ExitFloating(site) & "," _
& AdultsDying(site) & "," & Floating(site) & "," & Juveniles(site) & "," & MeanAgeRecruitment & "," & IncubationPeriod & "," _
& FledgingPeriod & "," & TwoFledge & "," & NestInitiationWeek_V & "," & RecruitSite(site, 1) & "," _
& RecruitSite(site, 2) & "," & RecruitSite(site, 3) & "," & RecruitSite(site, 4) & "," & Pred_C(site) & "," & Dispersal)

```

'get new estimates of survival parameters for next year

```
a = Rnd() : NestBeta(site) = oExcel.WorksheetFunction.NormInv(a, StartingNestBeta(site), SEMeanNestBeta)
B = Rnd() : ChickSurvivalAll(site) = oExcel.WorksheetFunction.NormInv(B, (StartingChickSurvivalAll + P_chicks(Pred_C(site) + 1)),
SEMeanDailyChickSurvivalAll)
Do Until ChickSurvivalAll(site) < 1
    B = Rnd(): ChickSurvivalAll(site) = oExcel.WorksheetFunction.NormInv(B, (StartingChickSurvivalAll + P_chicks(Pred_C(site) + 1)),
SEMeanDailyChickSurvivalAll)
```

Loop

```
C = Rnd()
```

```
Select Case site
```

```
Case Is = 3
```

```
    Z = oExcel.WorksheetFunction.NormInv(C, StartingZ(2), SEDailyAdultSurvivalAll)
```

```
Case Else
```

```
    Z = oExcel.WorksheetFunction.NormInv(C, StartingZ(1), SEDailyAdultSurvivalAll)
```

```
End Select
```

```
AdultSurvivalAll(site) = ((Math.Sin(Z) + 1) / 2) ^ (12 / 365) + 0.00001341271
```

```
If AdultSurvivalAll(site) >= 1 Then AdultSurvivalAll(site) = 1 - 0.00001341271
```

```
D = Rnd()
```

```
Select Case site
```

```
Case Is = 1
```

```
    JuvenileSurvivalAll(site) = oExcel.WorksheetFunction.NormInv(D, StartingJuvenileSurvivalAll(1), SEDailyJuvenileSurvivalAll)
```

```
Do Until JuvenileSurvivalAll(site) < 1 And JuvenileSurvivalAll(site) > (StartingJuvenileSurvivalAll(site) - (1 -
StartingJuvenileSurvivalAll(site)))
```

```
    D = Rnd()
```

```
    JuvenileSurvivalAll(site) = oExcel.WorksheetFunction.NormInv(D, StartingJuvenileSurvivalAll(1), SEDailyJuvenileSurvivalAll)
```

```
Loop
```

```
Case Else
```

```
    JuvenileSurvivalAll(site) = oExcel.WorksheetFunction.NormInv(D, StartingJuvenileSurvivalAll(2), SEDailyJuvenileSurvivalAll)
```

```
Do Until JuvenileSurvivalAll(site) < 1 And JuvenileSurvivalAll(site) > (JuvenileSurvivalAll(site) - (1 - JuvenileSurvivalAll(site)))
```

```
    D = Rnd()
```

```
    JuvenileSurvivalAll(site) = oExcel.WorksheetFunction.NormInv(D, StartingJuvenileSurvivalAll(2), SEDailyJuvenileSurvivalAll)
```

```
Loop
```

```

        End Select
    End Select
Next site

'Erase the values for summary statistics after one year
Select Case Jday
Case 182
    ReDim NestSum(Sites):          ReDim BroodSum(Sites):          ReDim ChickSum(Sites)
    ReDim FledgeSum(Sites):        ReDim DiesWhileFloating(Sites): ReDim RecruitorsSum(Sites)
    ReDim AdultsFloating(Sites):    ReDim ExitFloating(Sites):    ReDim AdultsDying(Sites)
    ReDim BreedingAdults(Sites):    ReDim SumSuccessfulBroods(Sites): ReDim Juveniles(Sites)
    ReDim AgeRecruitment(1000, Sites): ReDim TotalRecruited(Sites): ReDim RecruitSite(Sites, Sites)
End Select

If Jday = 365 Then Jday = 0 : Year = Year + 1 : Jday = Jday + 1
Select Case Week
Case 52
    If DofWeek = 8 Then Week = Week + 1 : DofWeek = 0
Case Else
    If DofWeek = 7 Then Week = Week + 1 : DofWeek = 0
End Select
DofWeek = DofWeek + 1: If Week = 53 Then Week = 1
Next Day : Debug.Print(boot & " " & sim)
Next boot

Select Case simulation_number
Case Is = 3
    Dispersal = Dispersal + 1 : If Dispersal = 7 Then Dispersal = 4 : SS = SS + 0.25
Case Is = 4
    Dispersal = Dispersal + 1
Case Is = 5
    SiteCounter = SiteCounter + 1
    Select Case SiteCounter
    Case Is = 5
        SiteSection = SiteSection + 4 : Dispersal = Dispersal + 1 : SiteCounter = 1 : If Dispersal = 7 Then Dispersal = 4
    End Select

```

```

Case Is = 6
    Dispersal = Dispersal + 1: If Dispersal = 7 Then Dispersal = 4 : target = target + 1 : If target = 5 Then target = 1
Case Is = 10
    Dispersal = Dispersal + 1: If Dispersal = 7 Then Dispersal = 4 : HabSite = HabSite + 1 : If HabSite = 5 Then HabSite = 1
End Select
Next sim
Beep() : FileClose((1)) : Debug.Print(Year & "," & Jday): Debug.Print("This thing is working")
End Sub
End Module

```